Logan River whirling disease study: factors affecting trout population dynamics, abundance, and distribution in the Logan River, Utah

by
Phaedra Budy
Assistant Professor
Assistant Coop Leader

Peter McHugh
Graduate Research Assistant

and

Gary P. Thiede
Research Associate

USGS Utah Cooperative Fish and Wildlife Research Unit
Department of Aquatic, Watershed, and Earth Resources,
and Ecology Center
Utah State University
Logan, UT 84322-5210

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TABLE OF CONTENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES

LIST OF FIGURES

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EXECUTIVE SUMMARY

During base flow conditions of 2001, 2002, and 2003, trout populations were sampled at eight sites ranging from Franklin Basin at high elevation to the Lower Logan site below the Logan River golf course. Population estimates were completed based on depletion techniques. Fish were weighed and measured, and condition was assessed. Subsamples of fish from each species and age group (adult or subadult) were tested for the presence of *M. cerebralis*, the parasite that causes whirling disease, using a polymerase chain reaction (PCR) technique. We also sampled a suite of abiotic (e.g., temperature) and biotic (e.g., periphyton) variables in all years and completed a species interaction experiment in 2003.

Since *M. cerebralis was* first detected in the Logan River in 1998, its range has broadened along the mainstem and most of its tributaries. Of the sites we sample regularly, Right Hand Fork is the only site that consistently tests negative for the presence of *M. cerebralis*. The average number of cutthroat trout testing positive for *M. cerebralis* has increased from 53.3% in 2001 to 71.2% in 2003 with more adults testing positive versus juveniles.

The prevalence (% positive) of *M. cerebralis* along the Logan River varies greatly within the basin, from 18% at Franklin Basin to 94% at Red Banks, for cutthroat trout. Differences in average summer temperature and discharge along the river explained most of the variability (>70%) in prevalence observed across sites. These results suggest that changes to stream temperature or discharge, either natural or anthropogenic, could alter the spread and impact of *M. cerebralis* in mountain streams.

Despite the high and growing rates of infection, we have not observed dramatic declines in the populations of cutthroat trout and brown trout in the Logan River and its tributaries. The abundance of fish overall is quite high; cutthroat trout average 952 fish/km ($\pm$ 675) and brown trout average 1662 fish/km ($\pm$ 1662) with wide variation across the eight sites. We do, however, see apparent but not significant, downward trends for both species at a majority of index sites.

Based on our experimental results as well as other observations, we conclude that the species zonation pattern observed in the Logan River is the result of a combination of biotic interactions (cutthroat trout) and physiological limitations (brown trout). Our experiment demonstrated that cutthroat trout could grow similarly well at both high and low elevation sites when reared in the absence of brown trout - a pattern that contrasts with their infrequent occurrence in the lower reaches and high abundance in the upper reaches of the river system. Further, our comparison of sympatric and allopatric cutthroat trout performance demonstrated that brown trout could have a considerable negative effect on cutthroat trout growth and condition. This effect was consistent across elevations and temperatures indicating that cutthroat trout do not attain competitive superiority even at low water temperatures.

INTRODUCTION

The Logan River, once considered one of the best trout streams in the region, still supports a popular fishery for stocked rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and the native Bonneville cutthroat trout (*O. clarki utah*). The decline in the population of the native Bonneville cutthroat trout throughout the intermountain west is evident, and only a few populations remain (Behnke 1992). However, the Bonneville cutthroat trout (hereafter referred to as cutthroat trout) in the Logan River might be one of the strongest and largest metapopulations within their historic range (Thompson et al. 2000). Many of the remaining cutthroat trout populations persist solely within headwater streams. Presently, the subspecies is recognized as an imperiled species by the American Fisheries Society (Williams et al. 1989) and is protected in Utah under an interagency conservation agreement; one of the primary goals of this conservation agreement is to better understand the role of introduced species in the decline and recovery of cutthroat trout - the focus of the research described herein. Brown trout of largely German and Scottish origin were introduced into Bonneville Basin streams in the late 1800s and are presently one of the most abundant trout species in the region. Simultaneously, cutthroat trout have disappeared from much of their range, presumably due to the combined effects of habitat degradation and introduced species. In addition, there is no evidence within this watershed that nonnative trout have expanded their populations within the past decades. Understanding the population dynamics and condition of the trout population, habitat quality, and the current and potential future effects of disease in the Logan River is critical for the effective management of this system (Lentsch et al. 1997).

Dynamics of fish populations are directly linked to the environmental characteristics of their habitat. Physical, chemical, and biological characteristics of the environment affect growth, survival, and birth rates. Further, salmonids use different habitats at different life stages and during different seasons (Bradford and Higgins 2001; Bonneau and Scarnechia 1998; Maki-Petays et al. 1997); therefore, it is necessary to expand habitat-population relationships to larger scales that encompass the various habitats used. Physical characteristics of habitat similarly affect the community structure and distribution of macroinvertebrate fauna and other biota. Hydrological and sedimentary networks within a drainage can explain, at least partially, the community organization of macroinvertebrate communities (Rice et al. 2001)

In addition to environmental variables, parasites and disease play an important role in determining fish population dynamics. The severity, prevalence, and impact of a given disease also depend on the interactions of several variables of the host, the pathogen, and environment (Reno 1998). Pathogens demand energy that the host would otherwise use for growth, survival, and reproduction (Minchella and Scott 1991). The occurrence of disease depends on the genetic characteristics, immunological, and nutritional conditions of the host, among other variables (Moffit et al. 1998). Diseases occur both in wild and cultured fish populations; however, while the effects of many diseases are known in cultured fish, less information is available for wild populations.

Myxobolus cerebralis, the parasite causative agent of whirling disease, has caused severe population-level declines in some states such as Colorado and Montana (Nehring and Walker 1996; Vincent 1996; Baldwin et al 1998); however, fish populations from other areas where fish have tested positive for whirling disease in other states (e.g., California) have not been significantly impacted. Fish samples for the Logan River have tested positive for whirling disease, but there is no evidence of population declines in this drainage at this time (Thompson et al. 2000, Budy et al. 2002).

Environmental factors also influence ecology of the tubuficid oligochaete, *Tubifex tubifex*. These worms are necessary as intermediate hosts, to complete the *M. cerebralis* life cycle. Several biotic and abiotic factors have been hypothesized to effect the survival and distribution of these tubifex worms based on laboratory experiments and field observations: (1) temperature (e.g., Reynoldson 1987), (2) substrate and aerobic bacteria (e.g., McMurtry et al 1983), (3) concentrations of nitrogen and phosphorus as well as bacteria (Letochova 1994), and (4) association with certain substrates and microflora (Lazim and Learner 1987).

Within *T. tubifex* worms, *M. cerebralis* transforms to an actinosporean (triactinomyxon gyrosalmo or TAM), which can infect salmonids. As with tubifex worms, the TAMs are thought to be affected by a suite of abiotic and biotic variables including: (1) temperature (e.g., El-Matbouli et al. 1999), (2) diel cycle, water flows, and temperature or timing of worm infection (e.g., Arndt et al. 2001), and (3) pH, water hardness, and dissolved oxygen levels (e.g., Smith et al. 2001)

Myxobolus cerebralis was reported for the first time in Utah in 1991. Other test samples have also demonstrated the presence of another pathogen (*M. neurobius*) related to the whirling disease pathogen. Possible effects of *M. cerebralis* on the native trout population in the Logan River are not yet known, nor are the physical, chemical, and biological characteristics that might be linked to its dispersal, infectivity, and prevalence. While trout and salmon samples from many systems throughout the

United States have tested positive for whirling disease, population level effects of the disease have been variable or unreported (Nehring and Walker 1996).

To evaluate population changes and the potential effects of whirling disease, we initiated (2001) a long-term monitoring program of the fish community at eight sites, from the upper headwaters of the Logan River (Franklin Basin) to the lower Logan River (Logan River golf course area; Figure 1). Survey locations were chosen to maximize information on trout distribution and capture the range of physical habitat characteristics observed in the Logan River drainage. Most selected sites were previously sampled by the Utah Division of Wildlife Resources (UDWR; *see* Thompson et al. 2000). This allowed us to compare and contrast our results to data from previous surveys. In addition, we considered different physical (e.g., flow, temperature, substrate), chemical (e.g., concentrations of phosphorous and nitrogen), and biological (e.g., productivity) factors associated with fish abundance and distribution, as well as the presence and prevalence of *M. cerebralis* along the stream.

However, to understand the diseases and their possible impacts on fish populations, it is crucial to determine which of the variables are important, how to measure these variables, and how to interpret the results of such measurements (Hedrick 1998). Numerous studies have focused on the biology of the parasite (Halliday 1976), the oligochaete host – *T. tubifex* (Hedrick and El-Matbouli 2002), and on the effects of fish (MacConnell and Vincent 2002). Surprisingly fewer studies have been designed to identify and enhance the understanding of the environmental factors that may be associated to the distribution, prevalence, and infectivity of the parasite (Hiner and Moffitt 2002).

Given this need, and given the variable effects of *M. cerebralis* on trout populations in different streams across the intermountain west, it is important to try and understand the role of environmental variation in determining the distribution and prevalence (percent infected) of *M. cerebralis* in newly infected watersheds. We investigated the relationship between a selected group of environmental factors and the distribution and prevalence of *M. cerebralis* in wild salmonid populations in the Logan River as part of de la Hoz Franco's (2003) MS thesis during the years of 2001-2002 of this study. We also compared results between PCR (polymerase chain reaction) analyses of wild fish (free ranging) and fish reared in sentinel cages. Those results indicated that despite its recent widespread distribution, the prevalence of the parasite varied greatly across sites. The lowest prevalence among cutthroat trout was found at the headwaters where the average summer temperature was below 9.5 ºC, whereas high prevalence was associated with temperatures above 12 ºC. Further, prevalence in brown trout and cutthroat trout increased with discharge reaching its highest levels at sites where the average base flow ranged between 0.7 and 1.1 m^3/s. Despite hypothesized mechanistic links to one or more stages or hosts in the M. cerebralis life cycle, we observed no relationship between M. cerebralis prevalence and substrate composition, nutrients (TN, TP), periphyton, and oligochaetes. However, multiple linear regression models that included average temperature and discharge explained most (>70%) of the variability in prevalence across sites for both species. This research has been summarized in de la Hoz Franco's MS thesis (de la Hoz Franco 2003) with the associated manuscript to be published in Transactions of the American Fisheries Society (de la Hoz Franco and Budy, *in press*).

Potential problems with nonnative fishes

In addition to threats from disease and habitat degradation, introduced fish species pose a considerable threat to the persistence of imperiled fishes throughout the western United States (Richter et al. 1997; Rahel 2000). Their effects can be unpredictable, but range from negligible to dramatic (Moyle and Light 1996a). The establishment of exotic fishes in streams typically causes three distinct patterns of native fish response. First and most extreme, nonnative fish species may cause the local extinction of a native species (Penczak 1999). Alternatively, they may integrate into the existing assemblage and cause no detectable effect (Wikramanayake and Moyle 1989) or cause subtle microhabitat use and/or territory size shifts in native taxa (Fausch and White 1981). Finally, native fish may be displaced from much of their range and thus relegated to an upstream refuge by nonnative fishes (Townsend and Crowl 1991). This third response category may cause a distinct pattern of species replacement from headwater to downstream reaches in an invaded river system.

While biologists have long been interested in patterns of species replacement along environmental gradients, there is a lack of information regarding this phenomenon in the context of native fish conservation and nonnative trout invasions. In streams with physical dispersal barriers, mechanisms permitting the persistence of native species in headwater reaches and exotic species in downstream reaches are clear (Townsend and Crowl 1991). In the absence of such barriers, however, attributes of recipient ecosystems or affected taxa that contribute to invasion limits and zonation patterns are poorly understood (Fausch 1989). Two models are offered to explain this pattern that could apply to stream ecosystems. First, exotic fishes can only invade as far as their physiological tolerance will permit (Moyle and Light 1996b). Under this scenario, upstream dispersal is possible, but abiotic factors limit reproduction and/or recruitment in newly invaded habitats. Second, condition-specific interactions between native and introduced species confer invasion resistance to native taxa at different levels of environmental variables (Dunson and Travis 1991). For instance, competition might be mediated by abiotic factors that parallel gradients along which species replacement occurs (e.g., water temperature; Taniguchi and Nakano 2000). Thus, one species dominates in competition at low temperatures while the other does so at cold temperatures (DeStaso and Rahel 1994). Under this model, nonnative fish species distributions are caused by a combination of biotic interactions and physiological limitations.

As exotic species limit the recovery of many imperiled fishes in the western United States (Richter et al. 1997) and their ranges continue to expand (Adams et al. 2002), identifying factors limiting alien and native species distributions in stream networks is of great conservation importance. For instance, an understanding of the limits to exotic species distributions may aid managers in manipulating habitats to favor a native species over an exotic one. In addition, such information could provide predictive insight into invasion extent in new streams or under an altered hydrology or climate scenario. Finally, investigations into such matters can yield information permitting more effective management of native trout in the presence of exotic trout sport fisheries.

Brown trout-cutthroat trout interactions in the Logan River

Fisheries scientists have long suspected that brown trout displaced cutthroat trout from much of their range through negative competitive interactions for several reasons. First, brown trout and cutthroat trout have a high degree of ecological similarity in wild populations, exhibiting similar preferences for prey resources and microhabitats (Budy et al. 2002). Also, brown trout exhibit strong territorial behaviors and intense intraspecific competition in their native range (Johnsson et al. 1999). Further, interspecific competition is widespread among other salmonid species, and has been demonstrated between brown trout and greenback cutthroat trout *(O. c. stomias*) in a laboratory setting (Wang and White 1994). Finally, while the majority of mountain stream networks were likely suitable for cutthroat trout historically, brown trout and cutthroat trout presently exhibit a high degree of spatial segregation in Bonneville Basin streams; brown trout occur primarily in downstream segments while cutthroat trout are most abundant upstream – a pattern which is particularly striking in the Logan River.

As part of de la Hoz Franco's (2003) MS thesis research, we evaluated the influence of biotic (e.g., competitors, parasite prevalence) and abiotic (e.g., temperature, discharge) factors on the distribution, abundance, and condition of salmonid fishes along the Logan River stream gradient (2001-2002). We observed a longitudinal change in fish distribution with native cutthroat trout and introduced brown trout demonstrating a distinct pattern of allopatry. Cutthroat trout dominated high elevation reaches, while reaches at lower elevations were dominated by brown trout. A transition zone between these populations was associated with consistent changes in temperature, substrate size, and dietary overlap. Variation in cutthroat trout abundance was best explained by a model including the abundance of brown trout and diel temperature (Adjusted R^2 = 0.80), whereas variation in brown trout abundance and distribution was best explained by a model including temperature and sediment size (Adjusted R^2 = 0.96). Thus, the cumulative evidence suggests that a strong potential exists for competition between these two fish species, yet this hypothesis has never been tested formally.

In addition to the uncertain potential for competition between cutthroat trout and brown trout, factors limiting the upstream limit of brown trout are unknown. These limitations are especially intriguing given that in some streams, brown trout distributions have remained remarkably stable for several decades (Brown 1935; Thompson et al. 1999). Vincent and Miller (1969) first studied this phenomenon and concluded that water temperature defined the upstream limit in Colorado streams. More recently, others have argued that brown trout invasion limits are not a simple function of stream temperature (Rahel and Nibbelink 1999), and have incorporated other physical variables (e.g., stream width) in their assessments of distributional limits. Ultimately, occurrence data suggest that air temperature, stream size, and biotic resistance (by native or nonnative trout) interact to limit the upper distribution of brown trout in streams (Fausch 1989). However, experimental data evaluating brown trout distributional limits are rare. For this reason, we conducted an experiment to evaluate how both brown trout-cutthroat trout competitive interactions and abiotic factors contribute to the observed allopatric distributional pattern existing in Utah streams.

Research objectives

The overall objectives of this study are to evaluate the population dynamics, abundance, and distribution of trout in the Logan River, and to determine the present and potential impacts of disease, habitat, and interspecific interactions on native Bonneville cutthroat trout. Concurrent with those objectives, we hope to evaluate and understand the mechanisms underlying the brown trout-cutthroat trout allopatric distributional pattern in the Logan River. Along those lines, our objectives were to: (1) experimentally test for a negative competitive interaction between cutthroat trout and brown trout in a field setting and (2) identify environmental variables (biotic and abiotic) that mediate interactions or affect the growth of each species when reared alone.

STUDY SITE

The headwaters of the Logan River are located in the southeastern corner of Franklin County, Idaho (Figure 1). The river runs southwest entering the state of Utah in the northeast corner of Cache County at an approximate elevation of 2600 m. The two largest tributaries are the Franklin Basin branch and the Beaver Creek branch, the first one being the largest; they join approximately 2 km south of Beaver Mountain, about 10 km south of the Idaho state line. The stream then runs through Logan Canyon for 64 km to reach the city of Logan, dropping to an elevation of approximately 1370 m at the eastern city limits (Thoreson 1949).

The gradient on the main stream varies from 7-32 m per km, and the higher gradient of the tributaries reach 75 m per km in Spawn Creek, making them predominantly white-water streams. Riffles and swift channels are common while pools are sparse. Boulders and rubble are common in the stream bottom of higher gradient sections; gravel beds and sand occur in areas of lower gradient or not exposed to the stream current, solid bedrock is also common. Impoundments are heavily silted as a result of natural erosion. The average discharge, based on a yearly average, is approximately 2.6 cubic feet per second (0.07 m^3/sec).

Predominant game fish include endemic Bonneville cutthroat trout, brown trout, stocked rainbow trout (including albino strains), brook trout, and mountain whitefish. Non-game fish include carp (*Cyprinus carpio*), mountain sucker (*Catostomus platyrhuncus*), and mottled sculpin (*Cottus bairdi*).

METHODS

Field sampling

Fish collections

Fish were collected during base flow conditions using a three-pass depletion technique. Block nets were placed at the lower and upper end of each stream section (100 m sections in the headwaters and tributaries, 200 m in the mainstem). The settings on the electrofishing equipment varied depending on the stream conductivity. Effort was recorded as the time spent fishing per fixed distance, as suggested by Reynolds (1996). For smaller streams, a backpack-mounted electrofishing unit was used. For the larger mainstream surveys, a canoe-mounted electrofishing unit was used.   Captured fish were anesthetized with a dose of MS-222. Lengths (mm total length, TL) and weights (g) were recorded for all fish, and in addition, fish were checked for external signs of whirling disease (e.g., black tail, deformities of the jaw or spine). When possible, 20 subadults and 10 adults from each species were kept. We classified subadult cutthroat trout as fish < 150 mm TL and subadult brown trout as fish < 180 mm TL.   These fish were euthanized using a lethal dose of MS-222 and placed on ice in labeled bags after lengths and weights were measured. These fish were used for diet, health condition assessment, PCR testing, and stable isotope analyses.

Condition analysis

Length-weight relationships (by species, both years combined; Appendix Figure 1) and condition factor (Fulton's $K = W * 100{,}000 / L^3$) were calculated for cutthroat and brown trout (adults and subadults based on length frequency data) for each site, and then compared within and across sites.

Diet analysis

To obtain a time-integrated measure of the feeding habits of and relations between brown and cutthroat trout in the Logan River, we took dorsal muscle tissue plugs from fish (between 150 – 250 mm TL) at three sites in 2003 for ^{15}N and ^{13}C stable isotope analysis. We took tissue from sites where each species lives alone (allopatry) and where they co-occur (live in sympatry); thus, we took tissue from 5 brown trout from Third Dam (Brown-Allopatry), 5 brown and 5 cutthroat trout from Twin Bridges (sympatry), and 5 cutthroat trout from Franklin Basin (Cutthroat-Allopatry). Tissue from each of these fish was dried at 60 ^{o}C, ground, encapsulated, and shipped to University of California at Davis for spectrometric analysis of the per mil content of nitrogen and carbon isotopes, relative to a standard. The content of ^{15}N gives insight regarding the trophic level (^{15}N increases with increasing trophic position) of each fish while the ^{13}C content provides insight into the source of carbon in a fish's diet (in streams, terrestrial carbon sources are lower in ^{13}C than aquatic-based carbon sources). Based on these considerations, we evaluated diet overlap and trophic positions of brown and cutthroat trout using graphical methods.

Population estimates

In 2003, we recalculated population estimates for this year and all previous years based on a generalized maximum-likelihood removal estimator calculated in Program MARK (White and Burnham 1999). In previous years, in order to compare to past UDWR estimates more directly, we relied on the Zippin method (based on least-squares regression), which uses only two of the three passes actually completed in our census. In addition to using the data from all three passes, the maximum-likelihood procedure in itself produces a more robust and consistent model and confidence intervals, thus giving us a more reliable indicator of the uncertainty regarding trout population estimates. Estimates were calculated based on an iterative approach, selecting combinations of capture probability and population size until the model that makes the data appear most likely is found.

Whirling disease analyses

For cutthroat and brown trout, fish heads from each specimen were removed, frozen, and tested for prevalence of *M. cerebralis* following the polymerase chain reaction method (PCR; Andree et. al. 1998). PCR samples were processed by Pisces-Molecular LLC (Boulder, Colorado).

Fish health condition assessment

Some of the same subsampled fish taken for PCR analysis were also assessed for health and condition using procedures outlined by Goede (1988, 1991). One technician conducted this profile for the entire sampling period.

Fish movement

In order to better understand fish movement between whirling disease "hot spots" and "clean areas", we marked trout species (target = 200 of each species) at each site with different colored site-specific Floy T-bar tags. Tagged fish were and will continue to be recovered from anglers (creel census and phone returns) and from the annual electroshocking survey in late summer. Informative signs were placed at the major fishing areas. The USU Fish Ecology Lab's phone number (435-797-3380) was imprinted on the fish tags.

In addition to fish movement data, a potentially important variable for understanding the spread of *M. cerebralis*, tagging will also allow us to determine growth of recaptured fish and will provide a corroborative comparison of abundance to depletion estimates of abundance.

Environmental variables

Sampling of river water for physical and chemical characteristics was generally conducted monthly through autumn.

Temperature- Temperature at each site was recorded hourly using temperature loggers (Onset Stow Away) set in streams.

Discharge- Discharge was measured using the recommended method of the U.S. Geological Survey. Thus, we measured depth and mean water column velocity at 20-30 locations along a cross-sectional transect at each site using a Marsh-McBirney Flow Mate 2000 electromagnetic flow meter. In addition to measuring discharge, we estimated stage-discharge relationships for Twin Bridges, Forestry Camp, Red Banks, and Franklin Basin based on water surface elevation recorded at Franklin Basin on the date of all discharge measurements; thus, we created a stage-discharge curve for use in the estimation of flow based only on the observed water surface elevation at the Franklin Basin bridge. All curves were fit using least-squares regression in SAS. Finally, in order to assess the flow variability throughout the year, we reconstructed the hydrograph for 2003 using daily flow measurements made at USGS gage number 10109000, immediately above First Dam.

Competition experiments

Experimental design

To assess the potential for a negative competitive effect of brown trout on cutthroat trout, we conducted field enclosure experiments in the Logan River from July through October of 2003. Using a regression-based experimental design, we replicated three treatments once at each of six systematically spaced sites along the natural elevational and thermal gradient present in the Logan River, in lieu of replicating treatments at any one site. Following a substitutive competition design (Fausch 1998a, 1998b), the three treatments were: (1) brown trout only (Brown allopatry); (2) cutthroat trout only (Cutthroat allopatry); and (3) half brown trout and half cutthroat trout (sympatry). In this way, we attempted to understand fish species performance when reared alone and in competition with the other species as it relates to environmental factors measured at the site- and/or cage-levels. Environmental variables were measured at each site using standard methods (Table 1).

At each site, we randomly assigned treatments to one of three 20-m^2 cages (6.0 x 3.3 m) made out of 12-mm black nylon mesh and fence (“T”) posts. All fish were stocked at ambient densities (a total of 8 fish/cage, 0.40 fish/m^2) using wild age-1 fish collected from allopatric locations in the Logan River (brown trout from Right Hand Fork; cutthroat trout from Franklin Basin and Beaver Creek). Prior to the start of the experiment, we weighed, measured, and tagged all fish with uniquely numbered Floy T-bar anchor tags. We subsequently monitored fish for any signs of shocking-, tagging-, or handling-related injury or mortality prior to the start of the trial. Following this period, we introduced fish into enclosures during early morning hours to avoid thermal stress.

Table 1. Measurement methods and assumptions used to quantify environmental covariates.

Variable (units)	Description level	Method/source	Comments & assumptions
Elevation (m)	site	USGS 7.5’ topographic maps	Surrogate for temperature.
Average, maximum, minimum and diel temperature (°C)	site	Temperature loggers	90-min intervals in a fast-flowing mid-channel location.
Discharge (cfs)	site	USGS-recommended method	Used Marsh-McBirney Flowmate 2000
Depth (cm)	cage	Measured in the center of each of twenty 1-m^2 cells inside enclosures using metered rod.	Collapsed to cage-level average.
Velocity (cm/s)	cage	Measured simultaneously with depth using flow meter.	Collapsed to cage-level average.
Start and End % Fines	cage	Assessed visually as the percent of the 20-m^2 cage area that was covered by fines (< 4 mm).	Assumed to account for sediment deposition due to cage effect.
Gravel size (mm)	cage	Median gravel size (*D*50) from Wolman pebble count.	Measured along 4 transects at start of experiment.
Prey count (no/m^2)	cage	Mean of three 30x30 cm Surber samples taken immediately upstream from enclosure	Assumes invertebrate drift source area is immediately upstream of cage.
Prey biomass (mg/m^2)	cage	Computed using count information and average length of taxa, with published length-mass relationships.	As above.

During the trial period, we cleaned debris from enclosures and inspected them for damage at a minimum of one time every other day. Results from a pilot study indicated that cleaning in this way ensured adequate delivery of invertebrate drift into enclosures. Following an initial 6-week trial, we removed all fish from enclosures for a summer growth measurement (early July to late August). To do this, we captured fish using a combination of low-voltage electrofishing and underwater (snorkelers with dipnets) methods. We subsequently weighed and then returned them to cages for an autumn trial period (through early October).

Performance measures

We quantified the performance of allopatric and sympatric brown and cutthroat trout using standard growth and condition metrics. Ending condition was assessed on an individual basis using percent relative weight, W_r,

$$W_r = (W / W_s) \times 100$$

where W is the observed weight of a fish at the end of the trial and W_s is the weight of the same fish as predicted from the respective length-weight relationship for Logan River brown or cutthroat trout (Budy et al. 2003).

Due to high tag loss rates throughout our experiment, we were unable to evaluate growth on an individual fish basis, and instead had to use cage-level weights in the computation for relative growth. Thus, relative growth, R, was computed as

$$R = [(W_2 - W_1) / W_1] \times 100$$

where W_1 and W_2 are cage-level median start and ending weights, respectively, for a given species. Prior to analysis, we summarized W_r at the cage-level (the experimental unit) for each species by treatment using both median and maximum values; R values were also summarized by species and treatment and then used directly in analyses as they were already estimated at the cage level.

Analysis

To assess the strength of interspecific competition, we compared growth, median relative weight, and maximum relative weight between allopatric and sympatric treatment groups for each species separately. To do this, we used analysis of variance (ANOVA) or, in situations where an environmental variable was highly correlated ($r > 0.60$) with the growth or condition of both treatment groups for a given species, we used analysis of covariance (ANCOVA) with that variable as a covariate. In addition, we assessed whether temperature limits the growth or condition and therefore the distribution of brown or cutthroat trout by examining allopatric treatment condition along an elevational gradient. Further, we examined sympatric fish performance within the same context in order to determine if temperature might mediate competitive interactions. All statistical analyses were performed using SAS software (SAS Institute 2003).

RESULTS

Field sampling

<u>Fish collections and population estimates</u>

Bonneville cutthroat trout, brown trout, rainbow trout, brook trout, and mountain whitefish were sampled during stream surveys in the Logan River drainage in summer 2003. We also captured a few sculpin at most sites and carp at the lower-most site. Based on maximum-likelihood population estimates, abundance and distribution of cutthroat trout, brown trout, and mountain whitefish varied in the Logan River (Figure 2, Table 2). Electrofishing catches were greater in 2003 versus 2002. Numbers of cutthroat trout per km decreased slightly at some sites and increased slightly at other sites from the 2002 survey (Figure 2). Numbers of brown trout per km increased or decreased depending on site compared to 2002 survey estimates (Figure 2). The following abundance summaries by site are based on maximum-likelihood removal population estimates. In addition, length frequency analyses are summarized by sample site.

Franklin Basin- Surveys indicated that cutthroat trout abundance has decreased steadily and significantly (ANOVA, F_2 = 247, P = 0.04) since 2001 (Table 2; Figure 2); however, 2003 estimates are similar to 1991 abundance estimates (Table 3; Figure 3). Using three-pass electroshocking, we captured 101 cutthroat trout ranging from 50 to 320 mm TL demonstrating at least five age classes (Figure 4). Unlike during our 2002 survey, we did not capture fish less than 50 mm, representing young-of-the-year (age-0) fish. Only one brook trout and one brown trout were captured at this site, precluding a population estimate.

Red Banks- As in past years, the cutthroat trout population estimate (1463 fish/km) was highest at this site (Table 2; Figure 2). Abundance has remained stable since 1991 (Table 3; Figure 3). Most of the fish captured were cutthroat trout (n = 264) in five possible age classes (Figure 4). Five brown trout were captured, yielding a population estimate of 28 fish/km, similar to estimates in past surveys (Table2; Figure 2). Only one whitefish (468 mm TL) was captured, therefore a population estimate was not calculated for this species.

Forestry Camp- We captured 226 cutthroat trout at this location providing a population estimate of 1323 fish/km (Table 2; Figure 2). Cutthroat trout abundance has fluctuated, but has remained at similar levels since 1991 (Table 3; Figure 3). Length frequency histograms indicate four potential age classes (Figure 4). Eleven brown trout in two age classes were captured, providing a population estimate of 53 fish/km, similar to the 2002 estimate for brown trout (Table 2). Only one brook trout (149 mm) was caught.

Table 2. Population estimates (Fish/km) and 95% confidence intervals (CI) made using the maximum-likelihood removal method in Program MARK. NA indicates that although a particular species was present at the site, insufficient catch precluded population estimation.

Site	Species	2001		2002		2003	
		Fish/ km	95% CI	Fish/ km	95% CI	Fish/ km	95% CI
Franklin Basin	Cutthroat	1695	1670-1730	1055	1042-1075	542	522-576
	Brook	44	43-52	46	36-107	NA	NA
Red Banks	Cutthroat	1601	1600-1607	2051	2021-2092	1463	1425-1514
	Brown	34	33-45	25	21-57	28	28-36
Forestry Camp	Cutthroat	1844	1835-1858	1420	1410-1436	1323	1277-1385
	Brown	NA	NA	58	58-58[a]	53	53-53[a]
Twin Bridges	Cutthroat	341	320-381	194	191-204	203	198-216
	Brown	446	434-467	513	494-546	446	442-456
	Whitefish	58	58-58[a]	NA	NA	NA	NA
Third Dam	Cutthroat	48	48-56	75	68-100	53	51-66
	Brown	2213	2162-2279	1394	1371-1426	1475	1467-1489
	Whitefish	NA	NA	178	175-187	70	68-79
Lower Logan	Brown	2317	1986-2802	901	879-934	732	705-774
	Whitefish	1274	629-3469	349	320-404	259	247-284
Temple Fork	Cutthroat	180	180-180[a]	558	524-612	361[b] 44[c]	334-412[b] 43-53[c]
	Brown	2261	2242-2288	2086	1900-2341	64[b] 106[c]	61-78[b] 85-174[c]
Right Hand Fork	Brown	3173	3115-3245	3804	3738-3884	2497	2397-2623

a. Confidence interval is unrealistically narrow due to irresolvable convergence problems in program MARK.
b. Estimate from reach surveyed upstream of newly built beaver pond within out original survey section.
c. Estimate from reach surveyed downstream of newly built beaver pond within our original survey section.

Table 3. Comparison of number of fish by species per kilometer for eight sample sites along the Logan River, Utah. Population estimates (Fish/km) and 95% confidence intervals (CI) were made using the maximum-likelihood removal method in Program MARK. Data prior to 2001 were taken from UDWR report 00-3 (Thompson et al. 2000) where estimates are based on reach-specific modified Zippin population estimates. Double dashes (--) indicate that no fish were captured or insufficient catch precluded a population estimate. All ages combined.

Site	Year	Population estimate (fish per km)			
		Species			
		Cutthroat	Brown	Whitefish	Rainbow
Franklin Basin	1991	634	--	--	--
	1999	1359	--	--	--
	2001	1695	--	--	--
	2002	1055	--	--	--
	2003	542	--	--	--
Red Banks	1991	1125	12	19	6
	1999	1083	--	--	--
	2001	1601	34	--	--
	2002	2051	25	--	--
	2003	1463	28	--	--
Forestry Camp	1991	1858	12	6	--
	1999	1361	5	25	--
	2001	1844	--	--	--
	2002	1420	58	5	--
	2003	1323	53	--	--
Twin Bridges	1991	199	236	68	50
	1999	86	155	54	--
	2001	341	446	58	--
	2002	194	513	--	--
	2003	203	446	--	--
Third Dam	2001	48	2213	--	--
	2002	75	1394	178	--
	2003	53	1475	70	--
Lower Logan	2001	--	2317	1274	--
	2002	--	901	349	--
	2003	--	732	259	--
Temple Fork	1967	50	56	--	--
	1999	194	284	--	--
	2001	180	2261	--	--
	2002	558	2086	--	--
	2003	361; 44[a]	64; 106[a]	--	--
Right Hand Fork	2001	--	3173	--	--
	2002	--	3804	--	--
	2003	--	2497	--	--

a. Because a beaver pond was constructed in the middle of the designated monitoring reach, we sampled a reach upstream (first number) and downstream (second number) of the original site.

Twin Bridges--Brown trout (446 fish/km) were more abundant than cutthroat trout (203 fish/km) at this site (Table 2; Figure 2), and abundance of both species has remained stable since 1991 (Table 3; Figure 5). We captured 88 brown trout of five apparent age classes (Figure 6). Thirty-nine cutthroat trout were captured, and only two whitefish (441 and 445 mm TL) were taken.

Third Dam--As in 2001 and 2002, Third Dam was the only site where rainbow trout (n = 5) and albino rainbow trout (n = 6) were captured: ranging from 195-272 mm. Brown trout were abundant (1475 fish/km) at this location, whereas abundance estimates of cutthroat trout (53 fish/km), and mountain whitefish (70 fish/km) were much lower (Table 2; Figure 2). We captured 291 brown trout in four possible age classes with modes at 55 mm, 155 mm, 230 mm, and 320 mm (Figure 6), similar to 2002 length frequencies (Budy et al. 2003). Ten cutthroat trout were captured: ranging from 130-260 mm (Figure 4). Thirteen whitefish were collected: three were juveniles (75-82 mm), the remainder ranged from 186-392 mm.

Lower Logan-- Brown trout dominated this section of the river (732 fish/km; Table 2; Figure 4); however, abundance has decreased dramatically since our first survey at this site in 2001 (2317 fish/km). One hundred twenty-two brown trout were captured in four possible age classes with modes at 70 mm, 160 mm, 230 mm and 300 mm (Figure 6). Only 39 whitefish were collected: 15 were smaller than 110 mm. Whitefish abundance (259 fish/km) in 2003 has decreased greatly since 2001 (1274 fish/km; Figure 2); however, it is important to note that whitefish appear to be quite sensitive to our shocking and handling techniques.

Temple Fork—A large beaver dam in the center of our study section (used in 2001 and 2002) forced us to modify our study section. One 100-m section was surveyed above the beaver dam, and another 70-m section was survey from the beaver dam to the confluence with the Logan River mainstem. In the “upper” 100-m section, we captured 31 cutthroat trout and 5 brown trout resulting in abundance estimates of 361 cutthroat trout/km and 64 brown trout/km. In the “lower” 70-m section, we captured 43 cutthroat trout and 76 brown trout resulting in abundance estimates of 44 cutthroat trout/km and 106 brown trout/km (Table 2; Figure 2). This was the only site at which cutthroat trout less than 50 mm were captured (Figure 4). In addition, 86% of captured brown trout were less than 100 mm.

Right Hand Fork--As in past surveys, only brown trout were captured (n = 316 in 2003) at this site, and since 2001, the abundance has held steady at nearly 3000 fish/km (Table 2; Figure 2), There appeared to be at least six possible age classes (Figure 6).

Overall, if we consider just our (Utah State University) fish survey data since the 2001 survey, cutthroat trout population estimates have decreased significantly at one site (Franklin Basin) and show apparent downward declines (but statistically insignificant) at 3 of the other 4 sites where they occur. Similarly, brown trout demonstrate apparent downward declines at five of the seven sites where they occur, with dramatic (three-fold) declines at the Lower Logan site. However, our estimates are similar to past UDWR fish survey data, suggesting no decline of either species from 1990's levels. Although whitefish appear to have declined, we suspect that this is a site-specific artifact of electroshocking.

Condition analysis

Contrary to past years, condition (Fulton's K) across size classes and between species was similar for cutthroat trout and brown trout captured in 2003. Subadult cutthroat trout average condition ranged from 0.96 $\pm$ 0.01 at Franklin Basin to 1.07 $\pm$ 0.02 at Forestry Camp (Figure 7). Adult cutthroat trout average condition ranged little: 0.98 $\pm$ 0.03 at Third Dam up to 1.03 $\pm$ 0.02 at Franklin Basin. Average condition of subadult brown trout ranged from 0.91 (n = 1) at Franklin Basin to 1.07 ± 0.001 at Temple Fork (Figure 8). Adult brown trout average condition ranged from 0.95 ± 0.03 at Third Dam to 1.10 ± 0.02 at Red Banks. Cutthroat trout and brown trout from the tributaries and mainstem exhibited similar condition.

Aging analysis

We aged scales on a subsample (n = 15) of cutthroat trout (150-320 mm TL; adults) captured in 2003. This preliminary aging analysis indicates a high degree of overlap in length-at-age for age-3 and age-4 fish; however, there is little overlap between age-2 and age-3 lengths (Figure 9). When more fish are aged and coupled with length frequency analysis, these data will provide more insight into age and growth determination.

Diet analysis

Our analysis of the stable isotope tissue content of brown and cutthroat trout yields some striking patterns in the feeding relations of these two species (Figure 10). First, there was very little overlap in dietary habits (i.e., there is no overlap on the isotopic content between species). Second, the isotope-based index of diet indicates that the feeding patterns are not heavily influenced by the presence of the other species; that is, allopatric cutthroat trout have a similar ^{13}C content as sympatric cutthroat trout (the same comparison is true for brown trout). Third, sympatric brown trout are enriched in ^{15}N, relative to their allopatric counterparts – indicating a higher degree of piscivory at these sites (i.e., more piscivory = more ^{15}N); this suggests the potential for predation on cutthroat trout, other fish, or cannibalism. Finally, the high degree of separation of both species on the ^{13}C axis suggests a greater reliance on terrestrially based carbon by cutthroat relative to brown trout. All of these results will be further validated with stomach content analysis in 2004.

Whirling disease analyses

Cutthroat trout--Clinical signs of whirling disease such as black tail or deformities were observed in very few trout. However, PCR assays for *M. cerebralis* indicated the parasite was present in all mainstem reaches sampled and in three tributaries: Temple Fork, Tony Grove Creek, and Little Bear Creek (Figure 11). Despite the widespread distribution of *M. cerebralis*, the prevalence of infection on cutthroat trout varied greatly, ranging from 18% at Franklin Basin to 94% at Red Banks (Figure 11). The average number of cutthroat trout testing positive for *M. cerebralis* has increased from 53.3% in 2001 to 71.2% in 2003 (Figure 12). More adults tested positive versus juveniles (< 150 mm TL), 76% and 53%, respectively (Figure 13).

Brown trout--Since 2001, *M. cerebralis* has not been detected in brown trout from Right Hand Fork. *Myxobolus cerebralis* was first detected in brown trout from Temple Fork in 2002; however was not detected there in 2003 (Figure 14). Percentage of brown trout that tested positive ranged from 31% at Twin Bridges to 100% at Red Banks. One new spot-testing site, near the Utah Water Research Lab, tested positive for *M. cerebralis* (Figure 14). The average number of brown trout testing positive has increased from 20% in 2001 to 36.4% in 2003 (Figure 12). A similar percentage of adults and juveniles tested positive for *M. cerebralis* (Figure 13).

Other salmonids--Prevalence of *M. cerebralis* was not tested in rainbow trout, mountain whitefish, or brook trout due to lack of funding. Samples that were taken are being held at the Fish Ecology Lab at Utah State University and will be analyzed if funds become available.

Fish health condition assessment

Health and condition (as based on UDWR HCP assessment) was assessed on 27 cutthroat trout, 33 brown trout, and one brook trout collected from 24 July to 30 July 2003 at Red Banks, Forestry Camp, and Lower Logan sites. We initiated this specific health and condition assessment in 2002; unfortunately a different assessor was used each year. Hemorrhagic eyes were observed in 26% of fish, versus 0% in 2002 (Budy et al. 2003). No gill or pseudobranch abnormalities were observed. One brown captured in the Lower Logan displayed hemorrhaging of the thymus. All but 13 fish had fat deposits around the pyloric ceca. Red coloration of the spleen was observed in 85% of cutthroat trout and 91% of brown trout. No fish had inflammations in the hindgut. Kidneys from two sampled fish were swollen. Thirty percent of fish had "non-red" livers. Bladders were empty in 85% of fish. Only one sampled fish was immature, 55% were females, and 45% were males. Four brown trout displayed malformed pectoral fins.

Fish movement

In the mainstem and two tributaries in 2002, we tagged 680 cutthroat trout and 846 brown trout with site-specifically colored, individually-numbered Floy T-bar tags (Table 4). To augment movement information, more trout were tagged in 2003 (Table 5). Recapture of tagged trout in 2003, indicated high site fidelity by cutthroat trout (40-100%) and even higher by brown trout (98-100%; Figure 15). Most cutthroat trout movement was in the upstream direction (e.g., Temple Fork to Red Banks), and was detected in the middle sections of the mainstem Logan River: Red Banks, Forestry Camp, and Temple Fork. Only one tagged brown trout moved, downstream from Third Dam (Figure 15). Although there were few tagged fish that moved, when fish did move, they traveled great distances. Cutthroat trout moved 500 m up to 9 km, and the lone brown trout mover traveled about 1 km (Figure 15). Although little movement was detected with tagged brown trout, one untagged brown trout was captured in Franklin Basin in 2003.

Table 4. Number of trout tagged in spring and summer 2002 by sample site in the Logan River, Utah. Only these tagged fish were used for movement information. Recapture summaries are also provided.

			Number of tagged trout	
	Site	Tag color	Cutthroat	Brown
Mainstem	Franklin Basin	Green	129	0
	Red Banks	Red	216	0
	Forestry Camp	Yellow	212	0
	Twin Bridges	Blue	23	89
	Third Dam	Purple	0	186
	Lower Logan	Gray	0	205
Tributaries	Temple Fork	Orange	100	103
	Right Hand Fork	White	0	263
		Total tagged in 2002	680	846
		Percentage of population tagged	9%	11%
		Electrofishing capture efficiency	55%	70%
		Total recaptured	175	212
		Fish recapture rate	26%	25%

Table 5. Number of additional trout tagged from 24 July to 19 August 2003 by sample site in the Logan River, Utah.

			Number of tagged trout	
	Site	Tag color	Cutthroat	Brown
Mainstem	Franklin Basin	Green	32	0
	Red Banks	Red	21	1
	Forestry Camp	Yellow	2	0
	Twin Bridges	Blue	20	18
	Third Dam	Purple	0	26
	Lower Logan	Gray	0	8
Tributaries	Temple Fork	Orange	10	0
	Right Hand Fork	White	0	22
		Total tagged in 2003	85	75

<u>Environmental variables</u>

Temperature- Average daily temperatures were coolest in the highest elevation site (Franklin Basin) and warmest at the lowermost site (Lower Logan; Figure 16). Average summer (June-September) temperatures at most sites (except for Franklin Basin) were close to or within the ideal range (10 to 13 °C) for growth of *T. tubifex,* the secondary host for *M. cerebralis*. From 2001-2003, average summer temperatures at the Lower Logan site were above this range (Figure 17; Appendix Figure 2). Mid-summer temperatures at Twin Bridges and Third Dam approached the ideal 15 °C for triactinomyxon (TAM) production (Appendix Figure 2). On the other hand, temperatures between 13 and 17 °C have been correlated with higher *M. cerebralis* infection rates in other studies. Our data indicate that only mid-summer temperatures at Forestry Camp, Twin Bridges, and Third Dam, and early and late summer temperatures at Lower Logan fell within this category. Temperatures at Franklin Basin were generally below ideal for TAM production, *T. tubifex* growth, and the temperature range that has been correlated to high infection rates (Appendix Figure 2).

Discharge--While minimum flows during the May-September period were similar to 2001 and 2002, both average and peak flows were considerably higher than those recorded at monitoring sites during previous years (Figure 18). This disparity arises primarily because not only was there a larger flood peak in 2003, but also because we took measurements at higher flows than we did in previous years (due to safety concerns). We were successful in estimating stage-discharge relationships for the four mainstem sites that are not influenced by irrigation diversions (Figure 19); the regression models explained the variation in flow as a function of water surface elevation at the Franklin Basin bridge well for all sites (Twin Bridges, R^2 = 0.97; Forestry Camp, R^2 = 0.97; Red Banks R^2 = 0.98; Franklin Basin, R^2 = 0.99; Figure 19). Finally, the 2003 Logan River hydrograph was characterized by a gradual rise to peak flow in mid-June followed by a rapid decline to base flow by the end of June (Figure 20). In addition, because base flow conditions were established early during summer 2003, we were able to conduct our electrofishing survey earlier than usual.

Competition Experiments

The first period (summer) of our competition trial was a considerable success despite some disturbance by humans, wildlife, and livestock, while our second period (autumn) suffered some fatal problems. During the summer period, we lost very few fish from enclosures in most cases. In only one instance was there so few fish remaining in an enclosure that we had to exclude it from our analysis (Twin Bridges, three fish were remaining); as a rule, we only excluded a replicate if it contained less than five trout (< 0.25 fish/m^2) at the end of a trial period. Due to fish loss that occurred during the fall period, however, more than half of all enclosures had to be withheld from our analysis. Losses were due to bird predation primarily, but humans may have played a role as well. In addition to predation problems, leaf litter caused excessive clogging in many enclosures causing some structural damage (e.g., tears in caging material). Therefore, results from the fall period have been withheld from analysis and the following discussion is based on the summer period only.

Allopatric growth patterns

Given that temperature is the variable that changed most predictably across enclosure sites (Table 1), patterns of allopatric fish performance observed indicate that summer conditions preclude neither brown trout from high elevation sites nor cutthroat trout from low elevation sites (Figure 21). Allopatric brown trout median relative weight ranged from 82% at Twin Bridges to 101% at Red Banks, while maximum W_r ranged from 87% at Chokecherry to 110% at Franklin Basin. In the absence of brown trout, cutthroat trout also grew consistently across all sites in the Logan River. Further, we saw no trend in growth of cutthroat trout that reflected their distributional pattern. However, they did suffer somewhat of a cage effect (i.e., $W_r < 100$ in most cases). Allopatric cutthroat trout median relative weights averaged 82% (range 77-88%), while maximum values generally averaged less than 100% and were highest at Franklin Basin (103%). Relative growth averaged 37% and 48% for allopatric brown and cutthroat trout, respectively (Figure 22), indicating substantial positive growth for both species in an enclosure setting. Ultimately, considering these trends in growth and condition as a function of elevation (a surrogate for temperature) indicates that summer growing conditions do not cause the observed zonation pattern (Figure 21).

Competitive interactions

While abiotic factors do not explain the zonation pattern observed in the Logan River, interspecific competitive interactions may explain the replacement of cutthroat trout by brown trout in the downstream direction. The presence of brown trout caused suppressed cutthroat trout growth and condition (median W_r, ANCOVA with discharge as a covariate, $F_{1,8} = 3.25$, $P = 0.101$, Figure 4; maximum W_r, ANOVA, $F_{1,9} = 9.58$, $P = 0.013$, Figure 22; relative growth, ANOVA, $F_{1,9} = 2.85$, $P = 0.126$, Figure 6). Specifically, cutthroat trout relative weight was 5-15% higher while relative growth was nearly 25% higher in the absence relative to the presence of brown trout. Conversely, the presence of cutthroat trout had a significant positive effect on median brown trout condition (ANOVA, $F_{1,9} = 5.68$, $P = 0.041$; Figure 23) and a slight positive effect on relative weight (ANCOVA using diel temperature as a covariate, $F_{1,8} = 1.89$, $P = 0.206$, Figure 22) and maximum W_r (ANOVA, $F_{1,9} = 1.57$, $P = 0.242$, Figure 24). Taken together, these results indicate that intraspecific competition is intense among brown trout, and more importantly, that they may be effective at competitively displacing cutthroat trout where they co-occur. Thus, our experiment provides direct evidence for biotic control on the downstream distributional limit of cutthroat trout, but no conclusive evidence regarding the upper brown trout limit.

DISCUSSION

Abundance and disease

Since *M. cerebralis* was first detected in the Logan River in 1998, its range has broadened along the mainstem and most of its tributaries. Of the sites we sample, Right Hand Fork is the only site that consistently tests negative for the presence of *M. cerebralis*. The average number of cutthroat trout testing positive for *M. cerebralis* has increased from 53.3% in 2001 to 71.2% in 2003 with more adults testing positive versus juveniles. Suspected vectors of the parasite include, fish eating birds, anglers' equipment, and fish (Taylor and Lott 1978; Bergersen and Anderson 1997; Schisler and Bergersen 2002). The diagnosis of *M. cerebralis* in wild and sentinel fish revealed that at some sites the parasite was not detected among sentinel trout, while highest prevalence rates were observed among wild trout. These inconsistencies suggest that fish movement is one of the vectors leading to the spread of the parasite along the stream and its tributaries. The observed differences in prevalence among juvenile and adult trout also support this hypothesis. A study conducted in a tributary of the Logan River demonstrated that the behavior of cutthroat trout ranges from almost completely stationary to frequent and wide-ranging movements (Hilderbrand 1998), depending on time and season, and life-history stage. From 2002-2003, cutthroat trout on the mainstem and in the Temple Fork tributary exhibited similar behavior, and infected fish could act as important vectors for the transport and spread of *M. cerebralis* spores to tributaries and headwaters.

Despite its widespread distribution, the prevalence of *M. cerebralis* along the Logan River varies greatly within the basin, from 18% at Franklin Basin to 94% at Red Banks, for cutthroat trout. This high variability in prevalence is not surprising; other studies have shown evidence of variability in prevalence and severity of infection across and within drainages (Baldwin et al. 1998; Hiner and Moffitt 2001). In this study, differences in average summer temperature and discharge along the river explained most of the variability (>70%) in prevalence observed across sites; hypothesized mechanisms that may explain this pattern are discussed in greater detail in de la Hoz Franco and Budy 2004. These results suggest that changes to stream temperature or discharge, either natural or anthropogenic, could alter the spread and impact of *M. cerebralis* in mountain streams.

The lack of clinical signs (e.g., deformities, black tail) in wild and sentinel fish suggest that the abundance of TAMs along the Logan River is low. Spore concentration (dose) is directly related to the development of clinical signs of whirling disease and its severity (Markiw 1992). However, other factors such as fish age (Markiw 1992), size (Thompson et al. 1999), species (Hedrick 1998; Sollid et al. 2002; Vincent 2002), and environmental factors at the time of the exposure may also influence the susceptibility of fish to the disease. Highly susceptible cutthroat trout fry could be exposed to low TAM concentrations during spring; low temperatures may also retard spore development and production, and flushing or diluting effects may result from high discharge during this season. Results from this study are consistent with the hypothesis formulated by Hubert et al. (2002) for cutthroat trout in spring streams of the Salt River drainage; that is their life-history patterns may reduce the susceptibility to *M. cerebralis* as fish migrate from the mainstem to smaller tributaries and headwaters to spawn, and fry use these lower water temperature streams as nursery habitat. These results point to the importance of rearing habitat (i.e., tributaries) to the overall health of the population.

Despite the high and growing rates of infection, we have not observed dramatic declines in the populations of cutthroat trout and brown trout in the Logan River and its tributaries. The abundance of fish overall is quite high; cutthroat trout average 952 fish/km ($\pm$ 675) and brown trout average 1662 fish/km ($\pm$ 1662) with wide variation across the eight sites. Although generally not statistically significant due to low power from only three years of data, if we compare 2001-2003, we do see apparent downward trends for both species at a majority of index sites. This downward trend in abundance was most notable for cutthroat trout at Franklin Basin, a headwater tributary site for cutthroat trout, and for brown trout at the Lower Logan site. Given the importance of the tributary sites for rearing habitat, and perhaps refuge from more infected mainstem areas (see above), the Franklin Basin site should be monitored carefully in the future. However, if we also consider data from past UDWR sampling, the population appears to be fluctuating quite a bit, but on average similar in magnitude compared to these earlier sampling events. Note, however, that differences in sampling techniques may hinder the comparability of these data to some degree. In addition, consistently worsening drought effects (especially in headwater streams such as Franklin Basin) and sluicing events from First Dam (above the Utah Water Research Laboratory) during dam reconstruction (October 2001) and in late summer 2002 may have contributed to declines in trout abundance.

Distribution and species interactions

The fish fauna of the Logan River are distributed longitudinally with a distinct allopatric pattern. Cutthroat trout dominated the mainstem headwaters and high-elevation reaches (altitudes above 1800 m), while brown trout dominated reaches at lower elevations of the mainstem and tributaries. Similar patterns of allopatry, zonation, and species addition along an altitudinal gradient have been documented in other studies (e.g., Fausch 1989), specifically for brook trout and other species (Gard and Flittner 1974), for brook trout, brown trout, and creek chub in Rocky Mountain streams

(Taniguchi et al. 1998), and for two char species in streams of Hokkaido Island, Japan (Fausch 1989). While these patterns of species change along longitudinal gradients may be common, the combination of biotic and abiotic factors, which drive them vary considerably across systems.

In previous work, we observed that the transition zone between the cutthroat trout and brown trout areas in our study corresponded to changes in environmental characteristics along the Logan River (de la Hoz Franco 2003). Cutthroat trout dominated the fish community in mainstem reaches with the lowest average minimum temperatures, highest diel temperature fluctuations, and where small boulders and large cobbles were the predominant substrate. In contrast, brown trout dominated reaches where the average minimum temperature was at least 1 ºC higher than at high-elevation reaches, diel temperature fluctuations did not exceed 6.2 ºC, and the primary substrate types were small cobble and coarse gravel. When these factors are considered together in a regression model, the best overall model predicting cutthroat trout abundance included the abundance of brown trout as an important factor, as well as diel temperature fluctuations. In contrast, the best overall model predicting brown trout density included diel temperature and sediment size. These results suggest that brown trout may have a significant effect on the longitudinal species distribution and on the abundance of the native cutthroat trout while the reverse does not appear to occur. These results were consistent with other studies that have provided evidence of abiotic factors (e.g., temperature, discharge or velocity, substrate) influencing the distribution and abundance of individual fish species (Lotrich 1973; Lobon-Cervia 2003), as well as the community composition (Hughes and Gammon 1987).

Based on our experimental results as well as other observations, we conclude that the species zonation pattern observed in the Logan River is the result of a combination of biotic interactions (for cutthroat trout) and physiological limitations (for brown trout). With regards to cutthroat trout first, our experiment demonstrated that they could grow similarly well at both high and low elevation sites when reared in the absence of brown trout - a pattern that contrasts with their infrequent occurrence in the lower reaches and high abundance in the upper reaches of the river system. Further, our comparison of sympatric and allopatric cutthroat trout performance demonstrated that brown trout could have a considerable negative effect on cutthroat trout growth and condition. This effect was consistent across elevations and temperatures indicating that cutthroat trout do not attain competitive superiority even at low water temperatures. Considering these results together, it appears that the general deficiency of Bonneville cutthroat trout in the lower reaches of the Logan River may be due to interspecific competition with exotic brown trout, demonstrating a biotic control on their distribution. It is uncertain why brown trout have not invaded the upper reaches of the Logan River and displaced cutthroat from these areas.

The existence of an upper distributional limit for brown trout, and thus a refuge for Bonneville cutthroat trout, is likely due to an abiotic factor affecting brown trout during another life stage and/or season. Three observations help support this case and suggest that the control operates somewhere during the period of egg deposition to the age-1 life stage: (1) the ability of sympatric and allopatric brown trout to perform well at both high and low elevation sites during the summer season suggests that neither summer temperatures nor biotic resistance by cutthroat trout prevents their establishment in high elevation areas; (2) a qualitative inspection of brown trout gonads at the end of the experiment suggests that brown trout have the potential to grow well enough to mature and ultimately spawn at high elevation sites; (3) there are no physical impediments to brown trout dispersal into high elevation sites, an observation supported by our own survey data (see previous section). Thus, brown trout can access and spawn at high elevation sites, but perhaps have not attained a high abundance in these reaches because of juvenile recruitment failure (between egg deposition and the life stage considered in our experiment). Given the concurrence of thermal changes and species replacement, it is most likely that temperature is the abiotic factor affecting recruitment. We caution, however, that these statements are hypotheses as much as they are conclusions. Ultimately, our conclusions regarding the controls on brown trout and cutthroat trout distribution limits in northern Utah rivers warrant further attention.

FUTURE

Monitoring

Monitoring of salmonid populations for abundance, distribution, and disease will continue in 2004, but at a reduced rate to reflect funding reductions. Disease analyses will occur at three or four of the eight index sites with fewer individuals tested per site. Abundance and distribution sampling and analysis will be the same as completed during the first three years of monitoring.

As part of another research effort funded by the Utah State University, Water Initiative, in 2004, we will also sample three index sites on the Bear River and some additional factors at three of our long-term index sites on the Logan River. The objectives and general approach for that work is as follows. *Objective 1*: Document and understand the abundance and distribution of trout in the Bear and Logan rivers (expanding a previous project from the Logan River into the Bear River proper). We will sample the fish community, the invertebrate community, and primary production at three sites in each river, ranging from the upper headwaters down to the lower, more degraded areas in the valley. *Objective 2*: Measure and evaluate the physical factors (temperature, discharge, etc.) that act to determine fish abundance, distribution, and health (e.g., disease, *see* de la Hoz Franco 2003). Fish sampled during this monitoring will be used to estimate abundance, will be evaluated for whirling disease (PCR), and will undergo health condition profiling. *Objective 3*: Use stable isotope ratios to develop an index of anthropogenically-derived nitrogen available at all trophic levels and to provide information on food web dynamics. Tracking nitrogen helps describe the importance and influence of water quality and land-use, and may be especially important for understanding differences in abundance and fish health at sites of varying habitat quality (Thompson and Luecke, *unpublished data*). Fish tissue samples, invertebrates, and periphyton will be analyzed for isotopic content, a measure of long-term diet composition and nutrient input. Stomach samples will be evaluated for short-term dietary composition. Temperature, discharge, turbidity, conductivity, and substrate will be measured monthly from May through October. Discharge and nutrient input, as key variables in many hypotheses about watershed function, were noted as important factors to measure and evaluate during discussions of "science questions and hypotheses" to be addressed in the Utah State University, Water Initiative, Bear River Laboratory Watershed. Monitoring data and research results will be synthesized in combination with results from the Logan River long-term monitoring project. Measures of periphyton, invertebrates, flow, turbidity, substrate, and temperature (described above) will be related to fish abundance, distribution, and health as well as land use and stream habitat quality. Ultimately, we will build a mathematical model to summarize the combined effects of biotic and abiotic factors in determining the present and future status of endemic cutthroat trout in these rivers and throughout their range.

Species interactions

A complete understanding of the potential role of exotic brown trout in both the decline and recovery of Bonneville cutthroat trout will require additional knowledge on the population-level importance of individual-level competitive interactions like those documented herein. Because intense individual-level interactions do not necessarily translate into a population-level response, this step is critical in understanding and mitigating for the impact of brown trout on cutthroat trout conservation efforts in Utah. We will address this need in 2004-2005 by conducting a large-scale field experiment in three small tributaries to the Blacksmith Fork River where the presence or absence of brown trout will be experimentally manipulated through electrofishing removal methods. Thus, using mark-recapture techniques, we will quantify and compare survival, growth, and emigration-immigration rates of cutthroat trout populations in the presence or absence of brown trout. This will provide us with insight regarding population processes critical to conservation efforts and allow us to fill knowledge gaps regarding the impacts of nonnative brown trout on the potentially imperiled Bonneville cutthroat trout. This research is funded largely by a 2004 Utah State University, Community-University Research Initiative (CURI) grant.

Diet analysis

In 2004, we will complete diet analysis for cutthroat trout and brown trout captured in the 2003 survey, and add diet analysis of trout captured in 2004 with emphasis on evaluating any diet differences between juveniles and adults for each species. In addition, we will compare stomach content analysis to stable isotope-based diet analysis.

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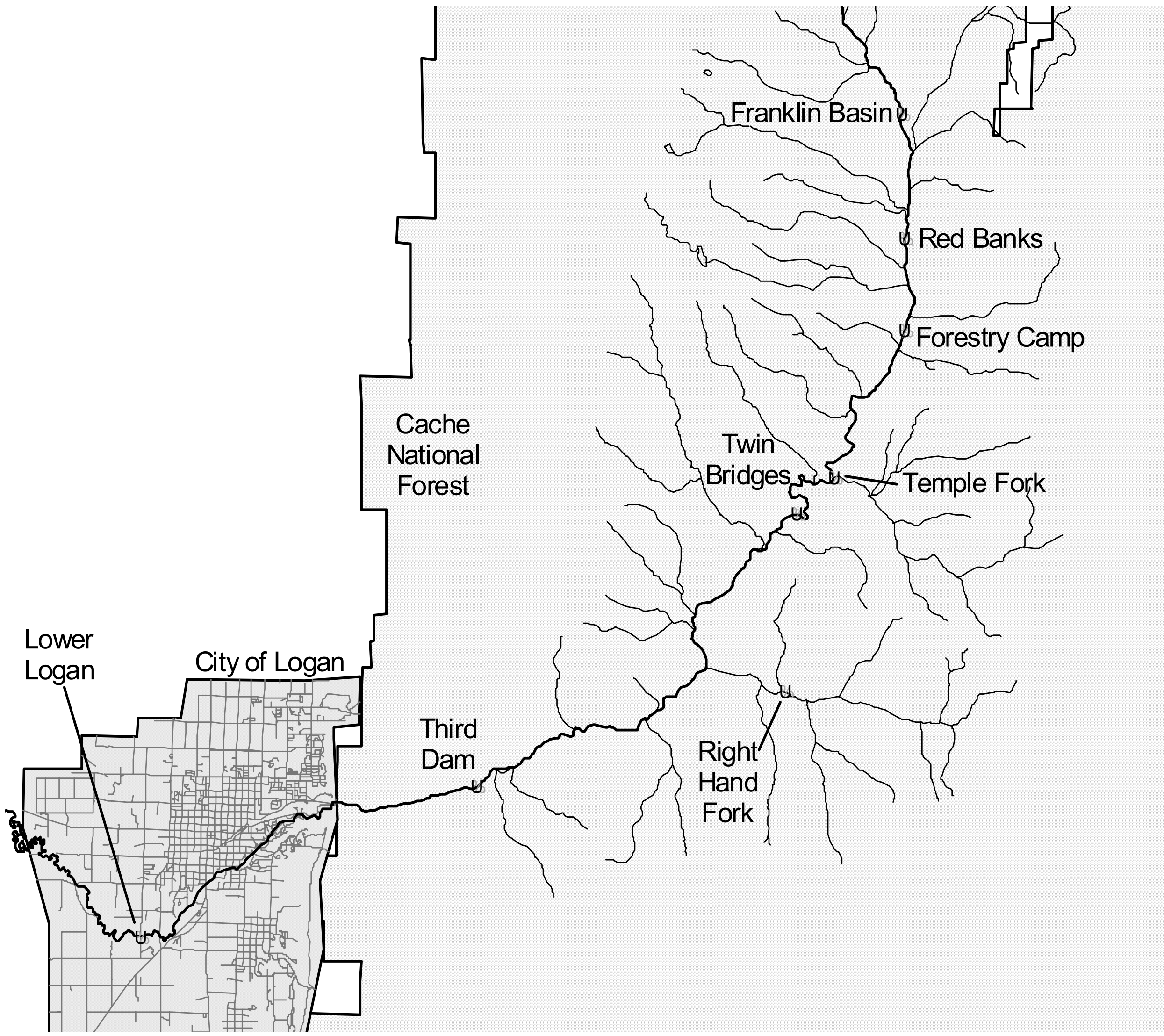


Figure 1. Map of the Logan River and sample sites.

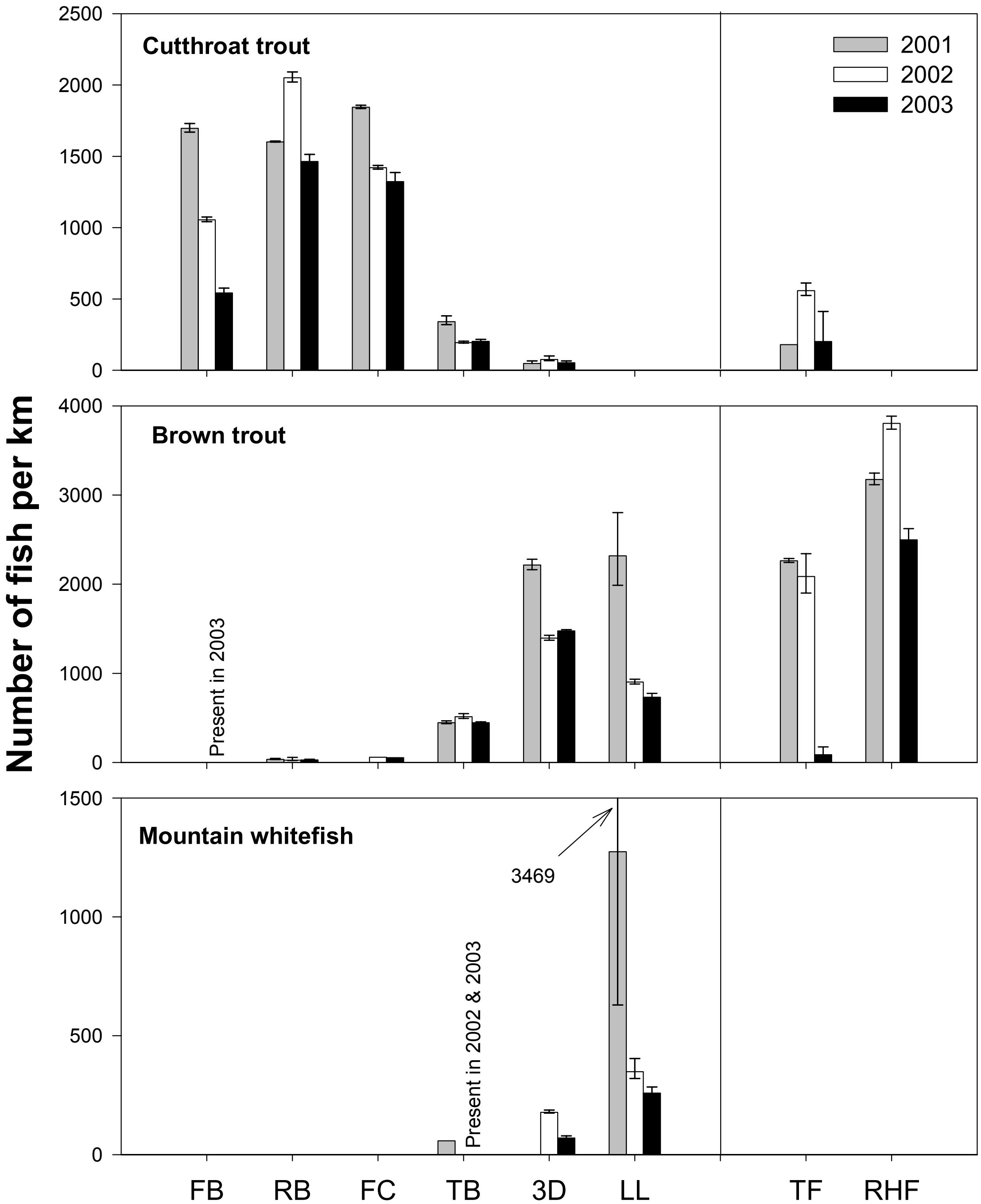


Figure 2. Population estimates for cutthroat trout, brown trout, and mountain whitefish based on the maximum-likelihood removal method in Program MARK, for six sites on the Logan River and tributaries (Temple Fork and Right Hand Fork), 2001-2002. Error bars represent 95% confidence intervals. FB = Franklin Basin, RB = Red Banks, FC = Forestry Camp, TB = Twin Bridges, 3D = Third Dam, LL = Lower Logan, TF = Temple Fork, RHF = Right Hand Fork. Note changes in y-axis scales.

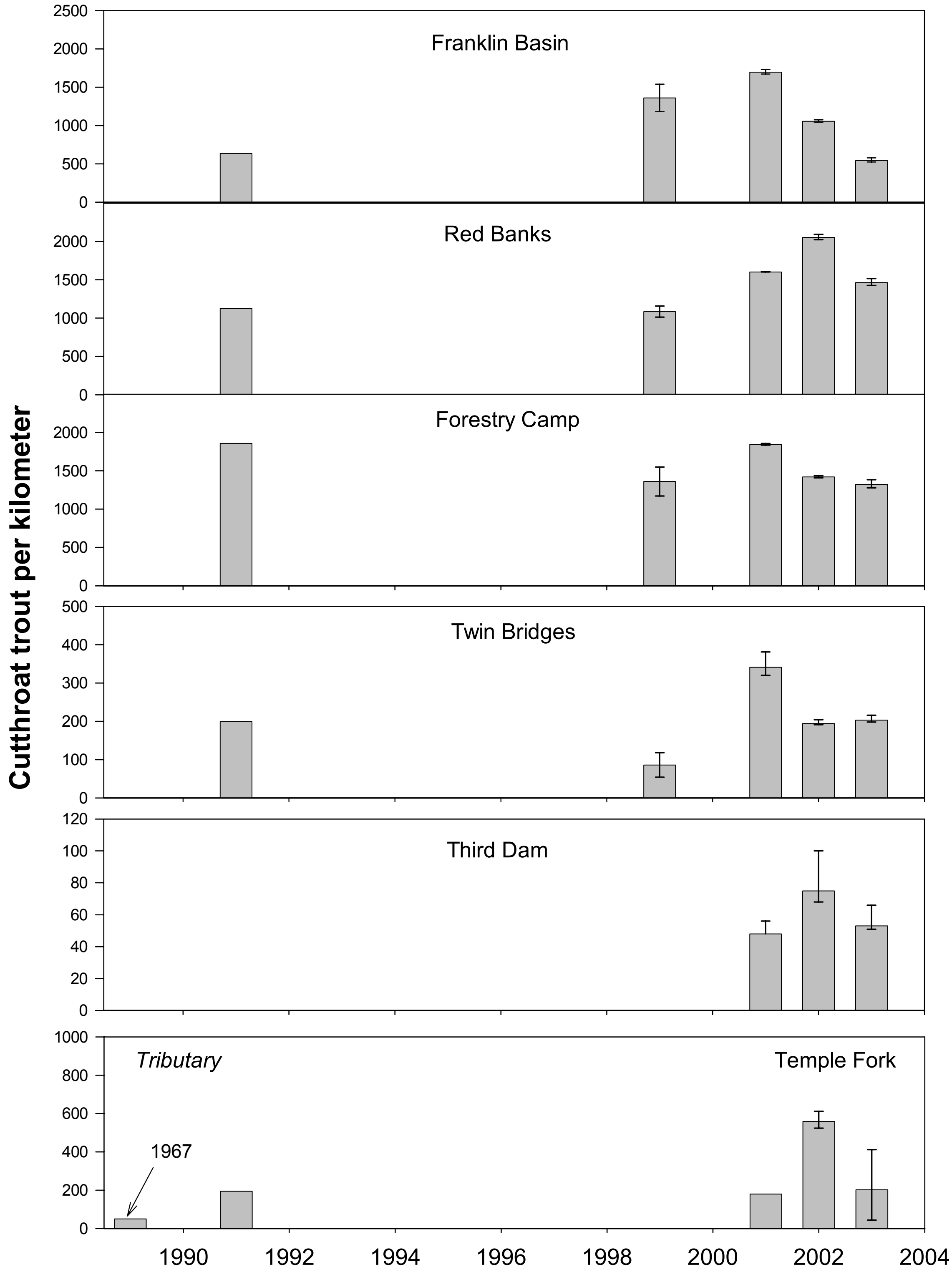


Figure 3. Population estimates for cutthroat trout at six sites on the Logan River, Utah based on the maximum-likelihood removal method in Program MARK (2001-2003 data) and a modified Zippin depletion method (1967-1999 data). Error bars represent 95% confidence intervals (2001-2003) or ± 2 standard errors (pre-2001 data). Note changes in y-axes.

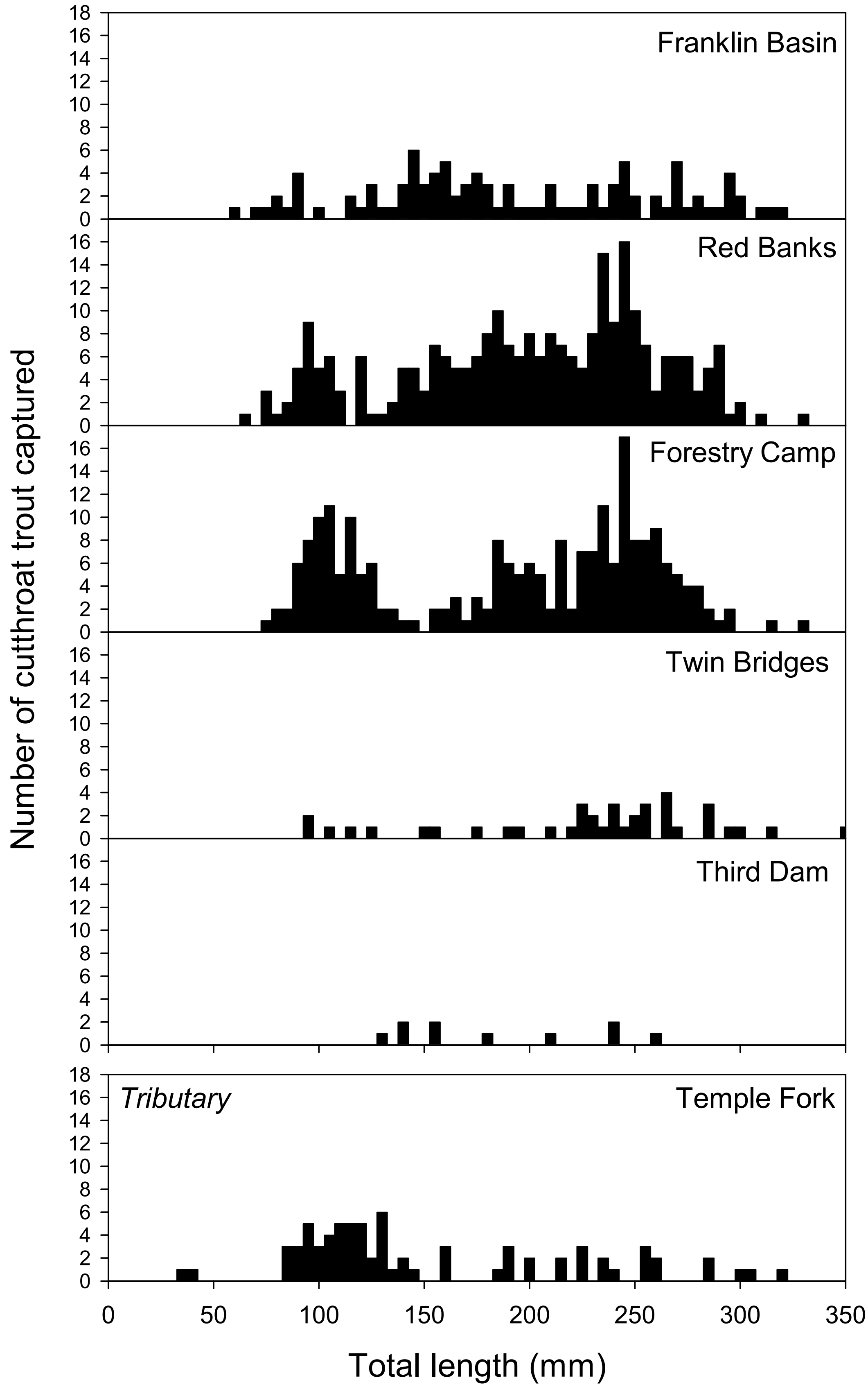


Figure 4. Length frequency distributions for cutthroat trout captured by electrofishing at five sample sites along the Logan River and one tributary, 2003.

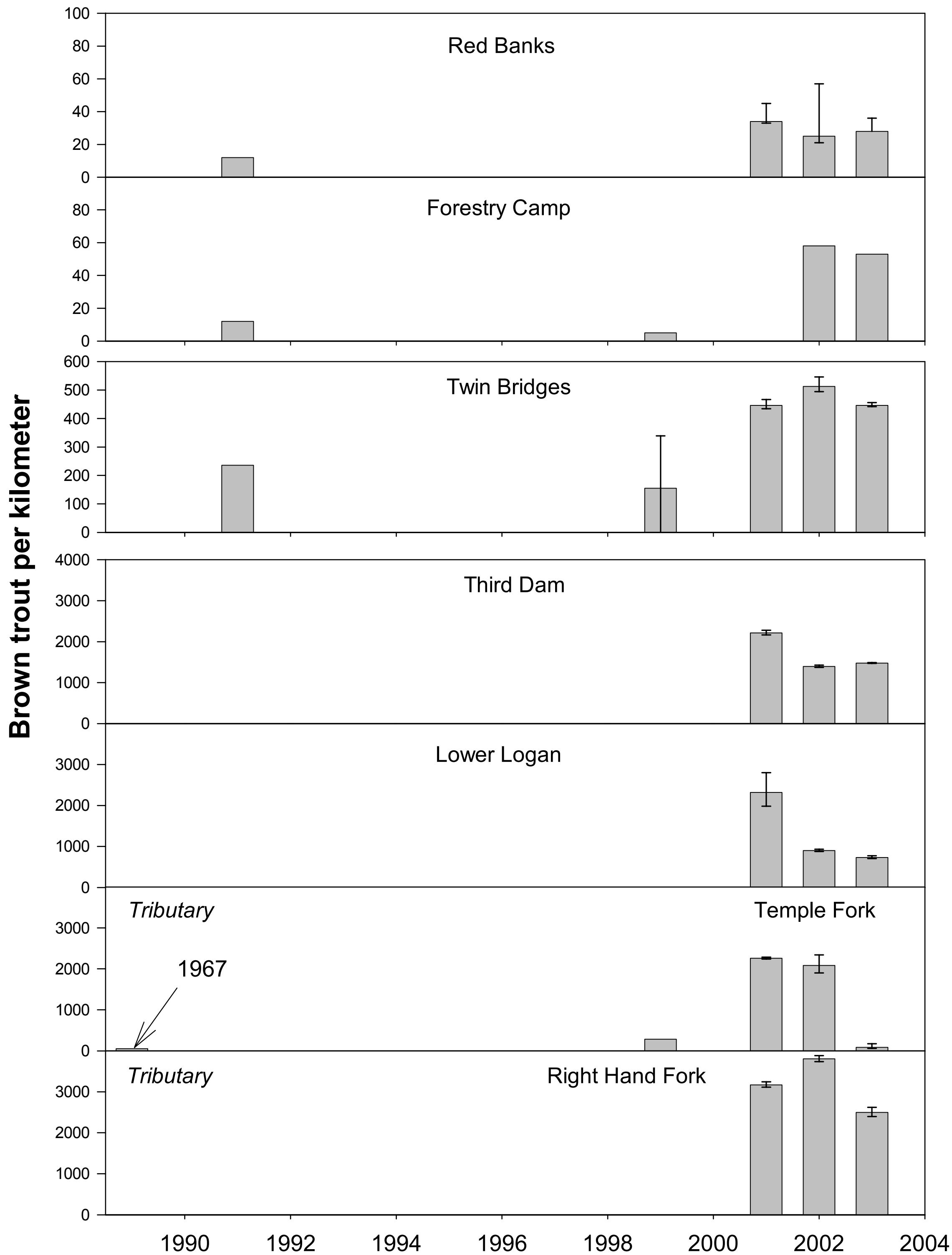


Figure 5. Population estimates for brown trout at seven sites on the Logan River, Utah based on the maximum-likelihood removal method in Program MARK (2001-2003 data) and a modified Zippin depletion method (1967-1999 data). Error bars represent 95% confidence intervals (2001-2003) or + 2 standard errors (pre-2001 data). Note changes in y-axes.

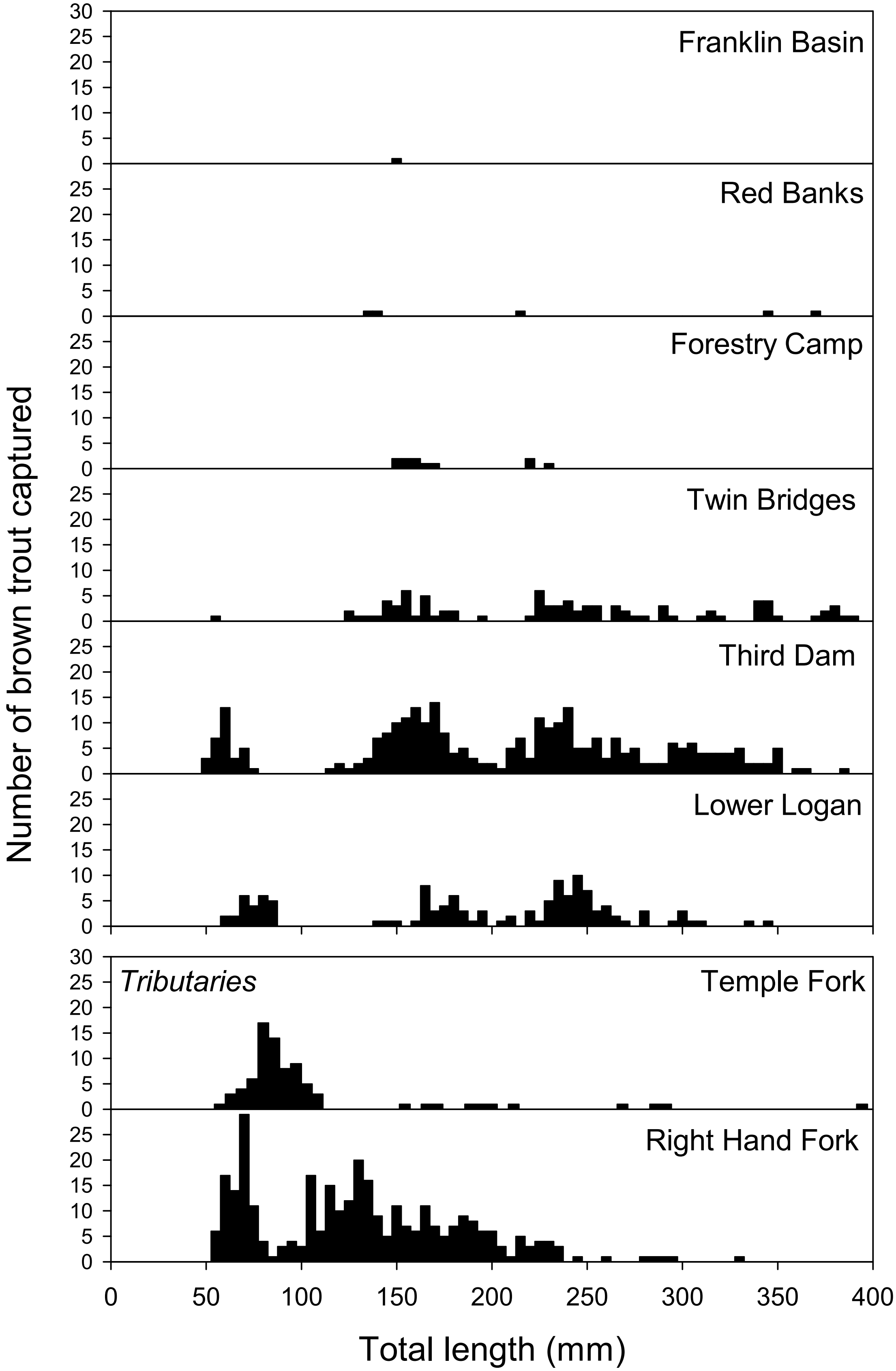


Figure 6. Length frequency distributions for brown trout captured by electrofishing at six sample sites along the Logan River and two tributaries, 2003.

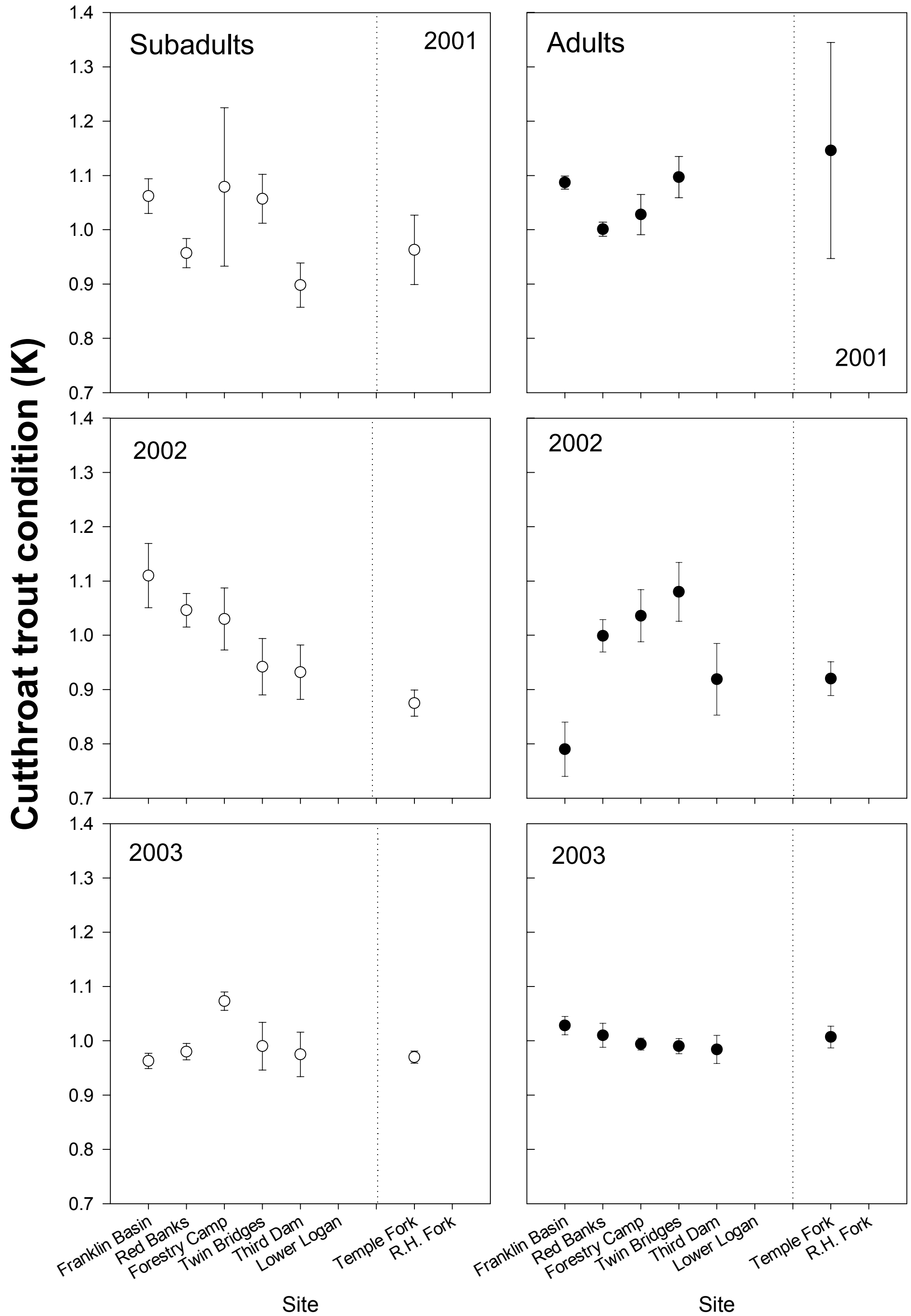


Figure 7. Condition (Fulton's K) of adult and subadult cutthroat trout captured in the Logan River and two tributaries, 2001-2003. Error bars represent ± 1 standard error.

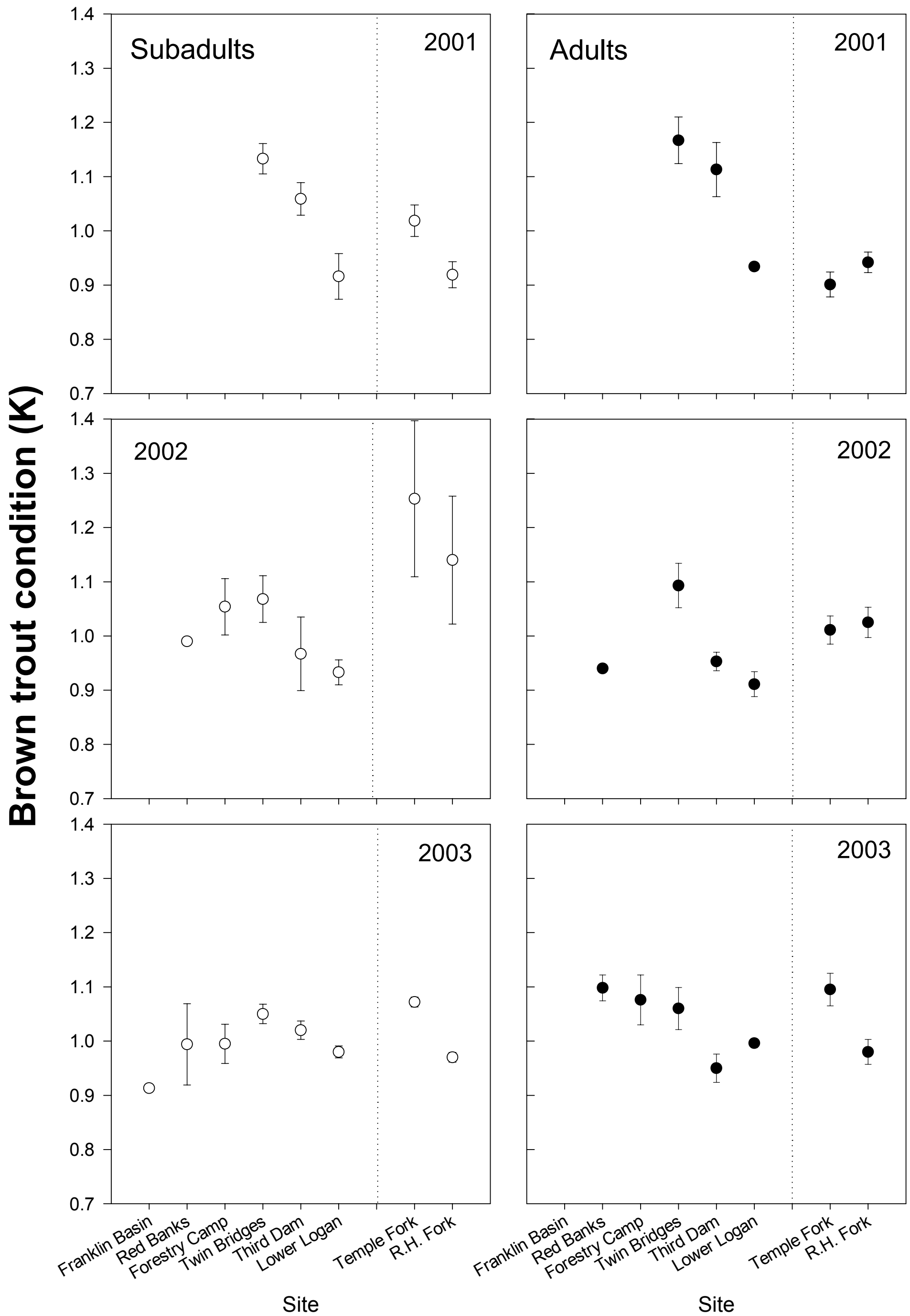


Figure 8. Condition (Fulton's K) of adult and subadult brown trout captured in the Logan River and two tributaries, 2001-2003. Error bars represent ± 1 standard error.

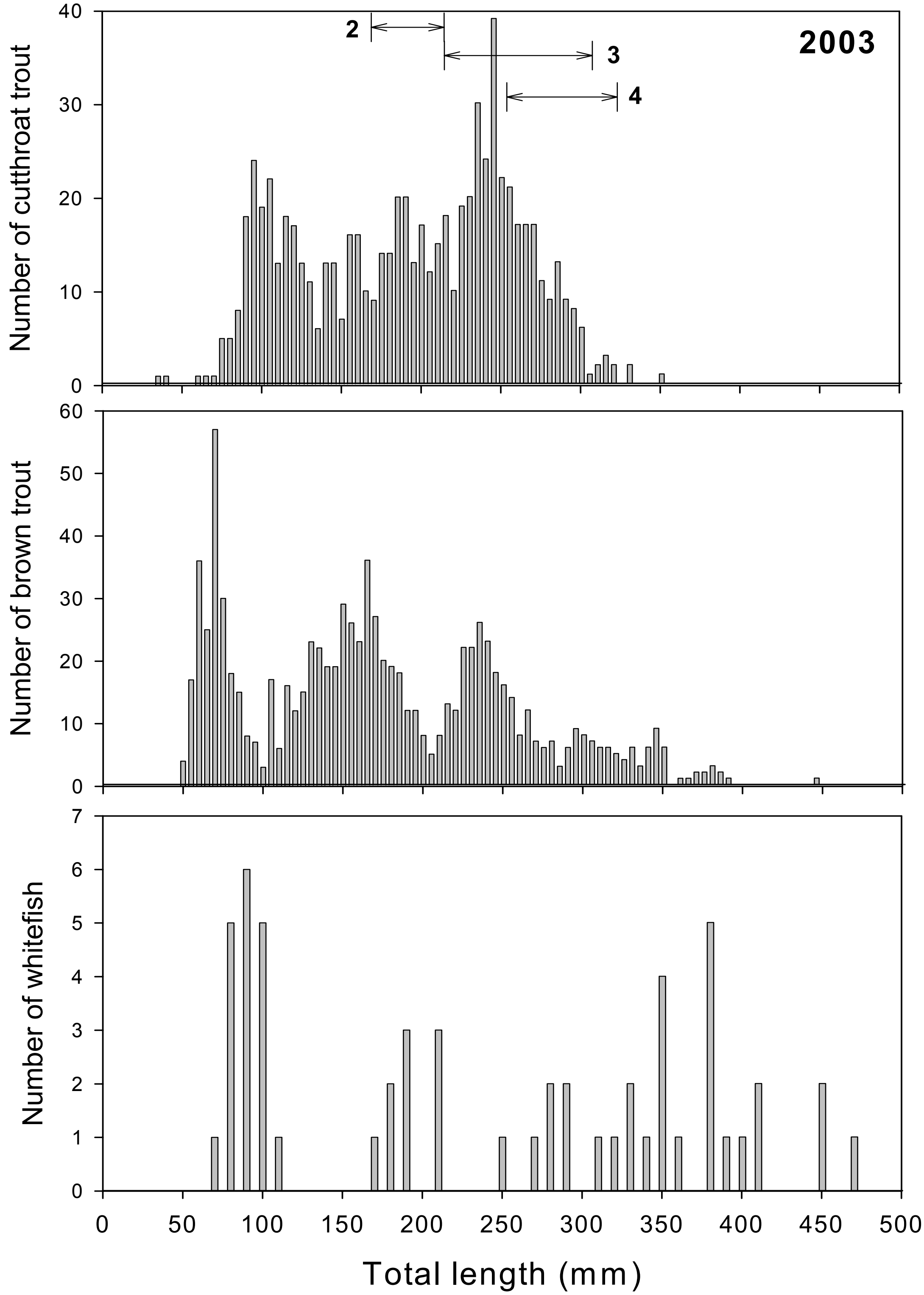


Figure 9. Length frequency distributions for cutthroat trout, brown trout, and mountain whitefish captured by electrofishing at six sample sites along the Logan River and two tributaries, 2003. All sample sites are combined. Number and range on top panel indicates length range for specific ages (2, 3, and 4) of cutthroat trout (n = 15). Note changes in y-axis scale.

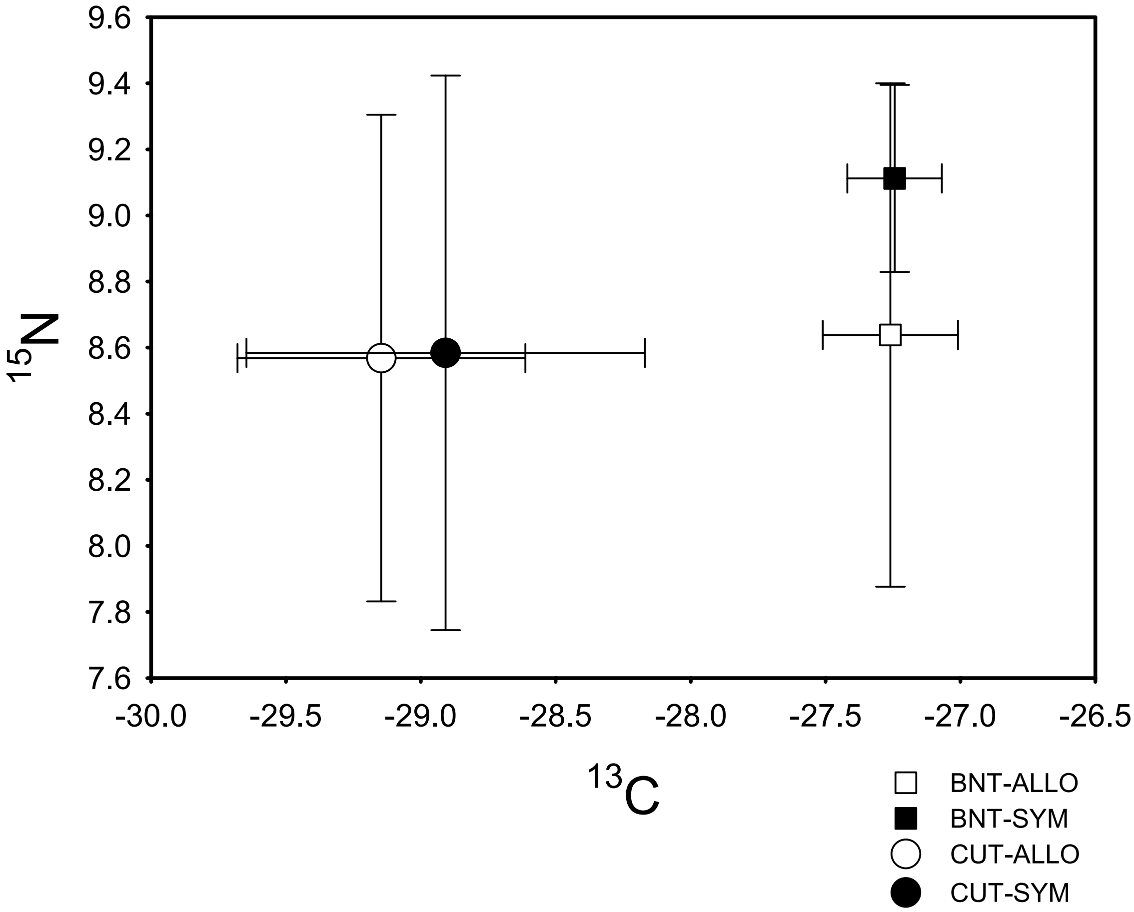


Figure 10. Plot of δ^{15}N ($\pm$ 2 standard errors, *SE*) against δ^{13}C ($\pm$ 2*SE*) for allopatric (open symbols) and sympatric (filled symbols) brown trout (squares) and cutthroat trout (circles) from the Logan River, 2003. Allopatric brown trout (*n* = 5) were collected at the Third Dam site; allopatric cutthroat trout (*n* = 5) were collected at the Franklin Basin site. Sympatric brown (*n* = 5) and cutthroat trout (*n* = 5) were both collected at the Twin Bridges site.

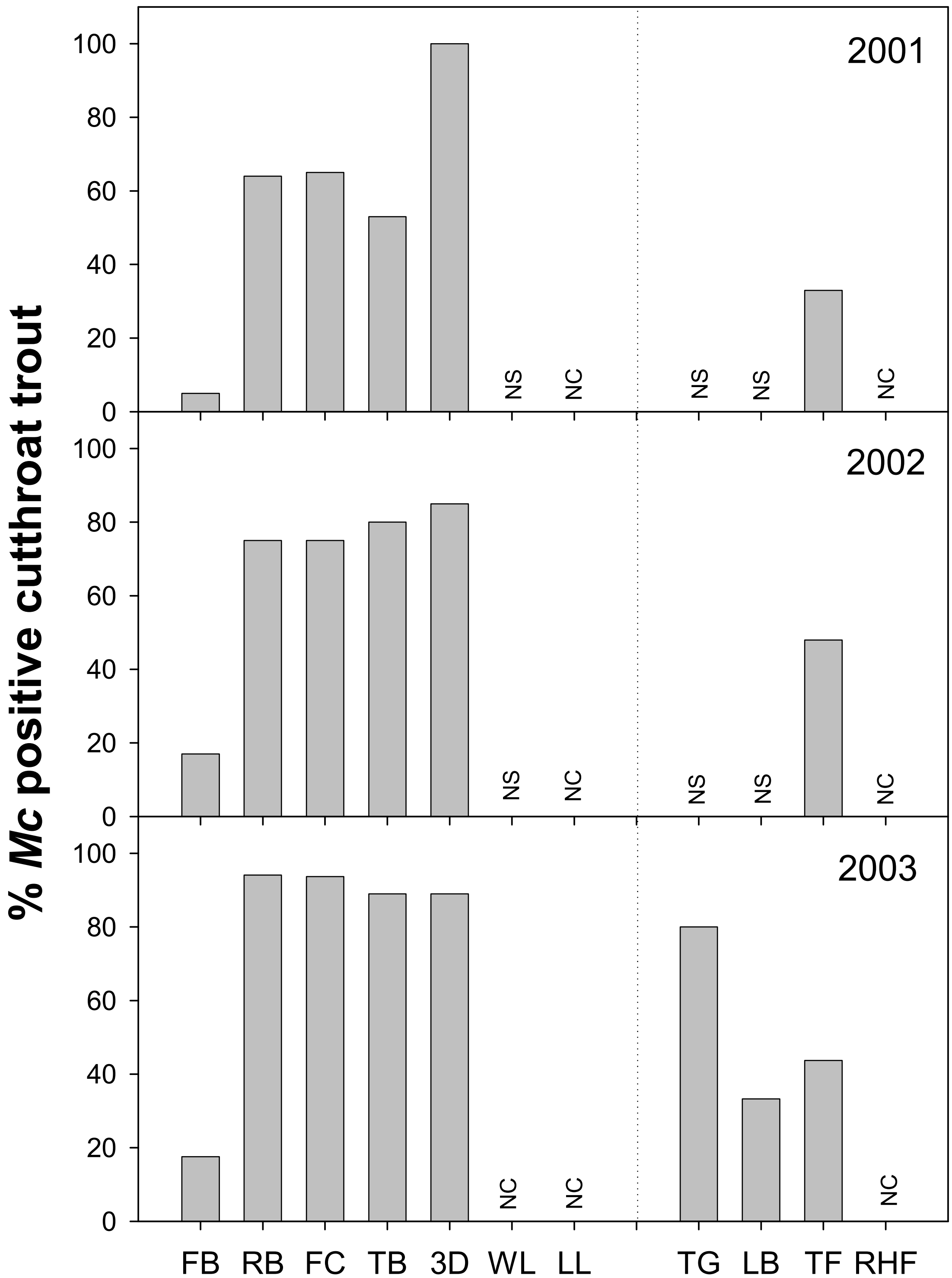


Figure 11. Mean percentage of cutthroat trout (all ages combined) by sample site that tested positive for *M. cerebralis* in the Logan River, 2001,2002, and 2003, based on PCR testing. NS = site not sampled. NC = none captured. FB = Franklin Basin, RB = Red Banks, FC = Forestry Camp, TB = Twin Bridges, 3D = Third Dam, WL = Water Lab, LL = Lower Logan, TG = Tony Grove, LB = Little Bear, TF = Temple Fork, RHF = Right Hand Fork.

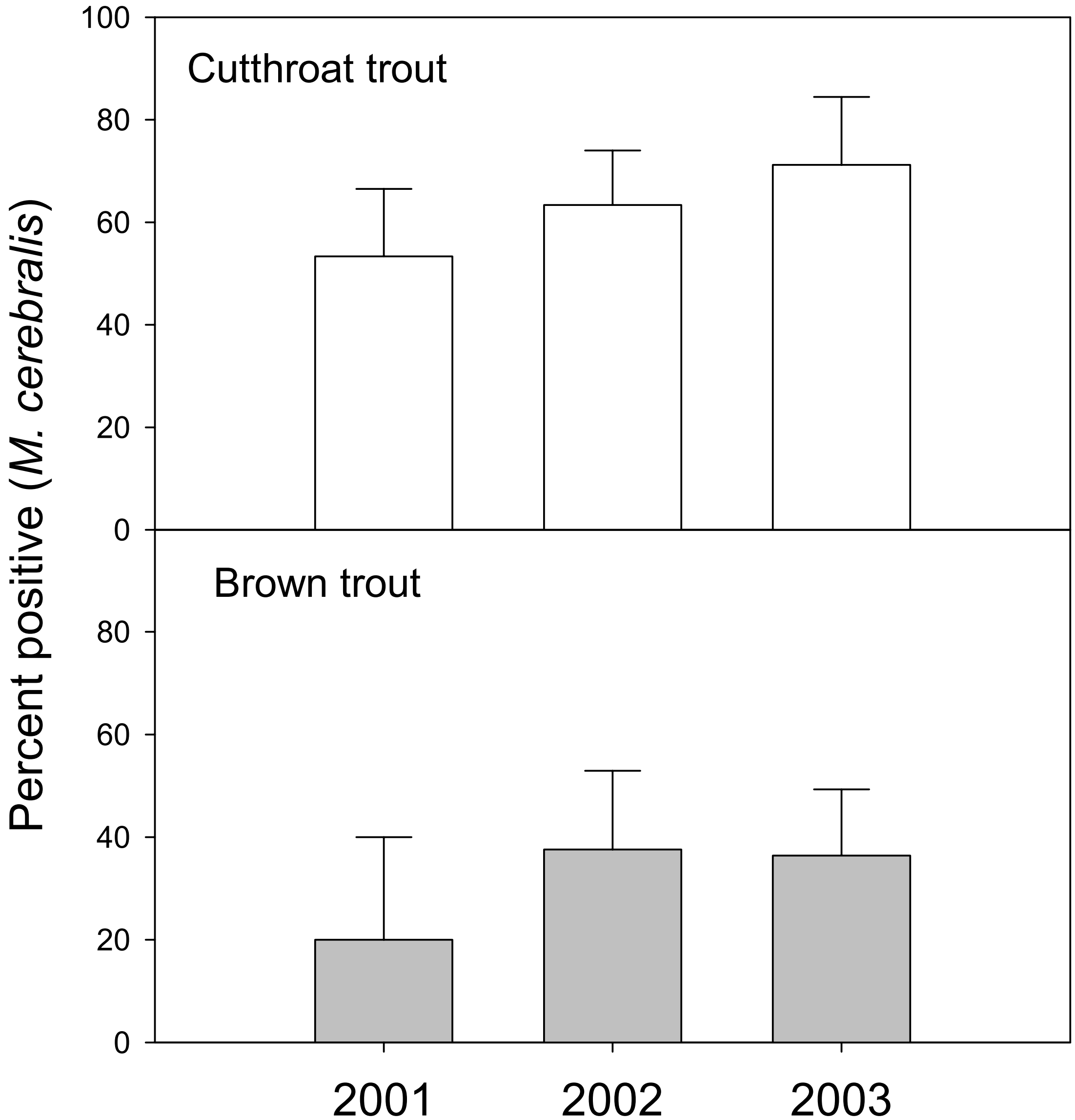


Figure 12. Mean percentage of cutthroat trout and brown trout (all ages and sites combined) that tested positive for *M. cerebralis* in the Logan River, over a 3-year period, based on PCR testing. Error bars indicate one standard error.

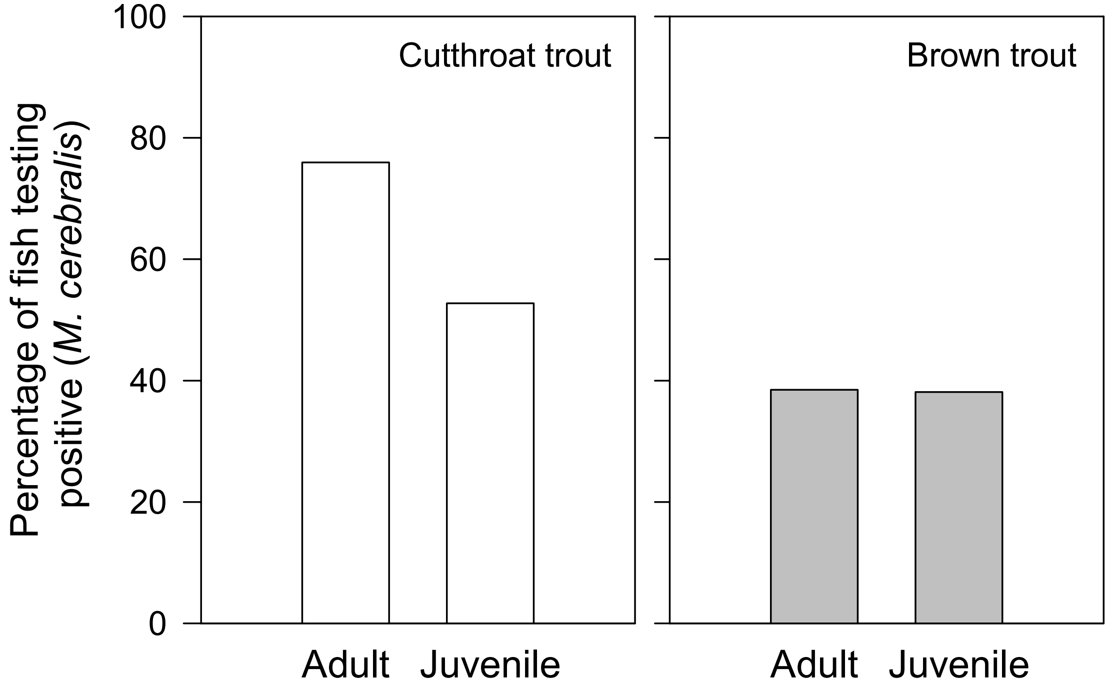


Figure 13. Mean percentage of cutthroat trout and brown trout (all sites combined) by size class that tested positive for *M. cerebralis* (based on PCR testing) in the Logan River, over a 3-year period.

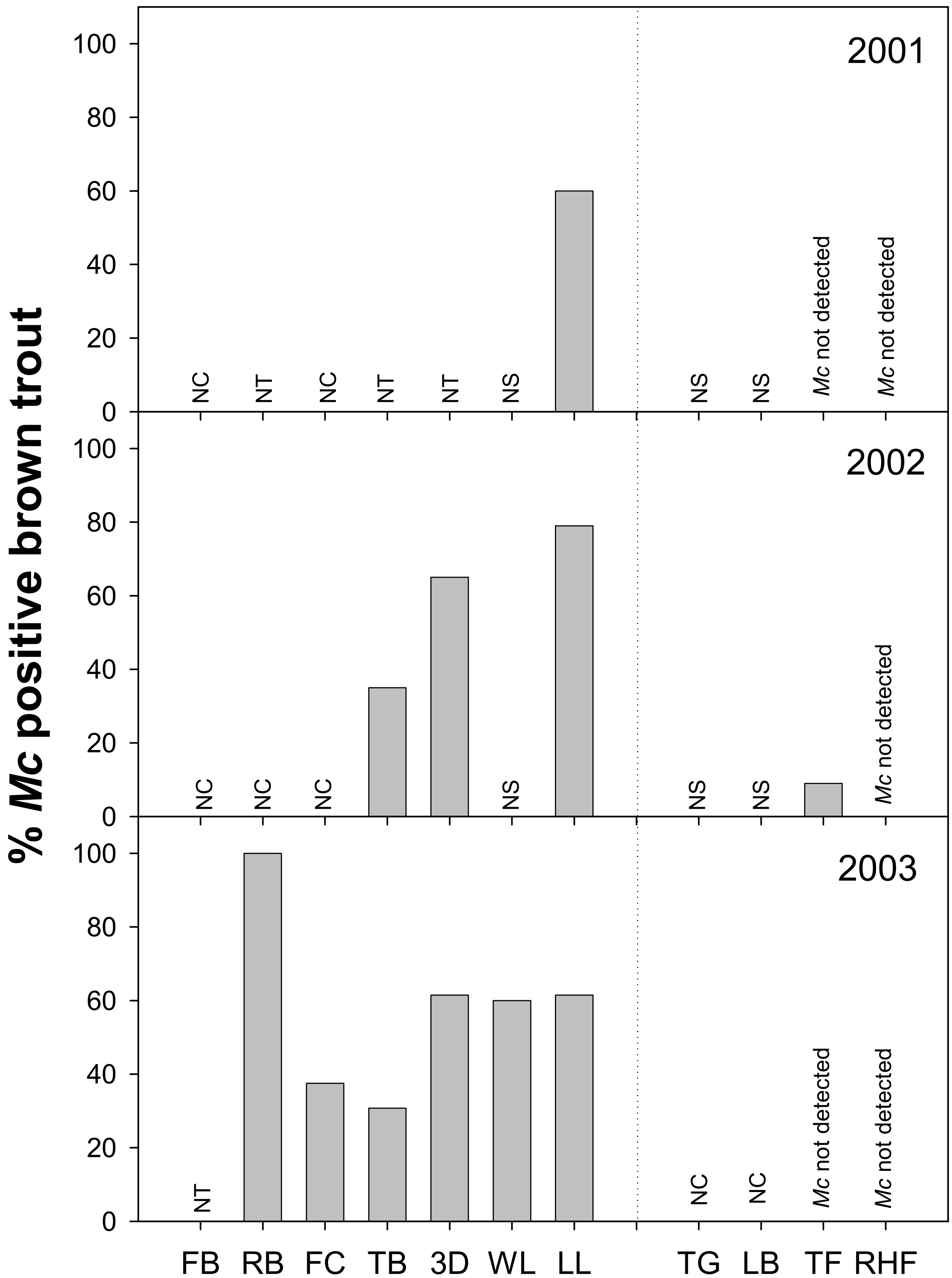


Figure 14. Mean percentage of brown trout (all ages combined) by sample site that tested positive for *M. cerebralis* (based on PCR testing) in the Logan River, 2001, 2002, and 2003. NS = site not sampled. NC = none captured. NT = samples not tested. FB = Franklin Basin, RB = Red Banks, FC = Forestry Camp, TB = Twin Bridges, 3D = Third Dam, WL = Water Lab, LL = Lower Logan, TG = Tony Grove, LB = Little Bear, TF = Temple Fork, RHF = Right Hand Fork.

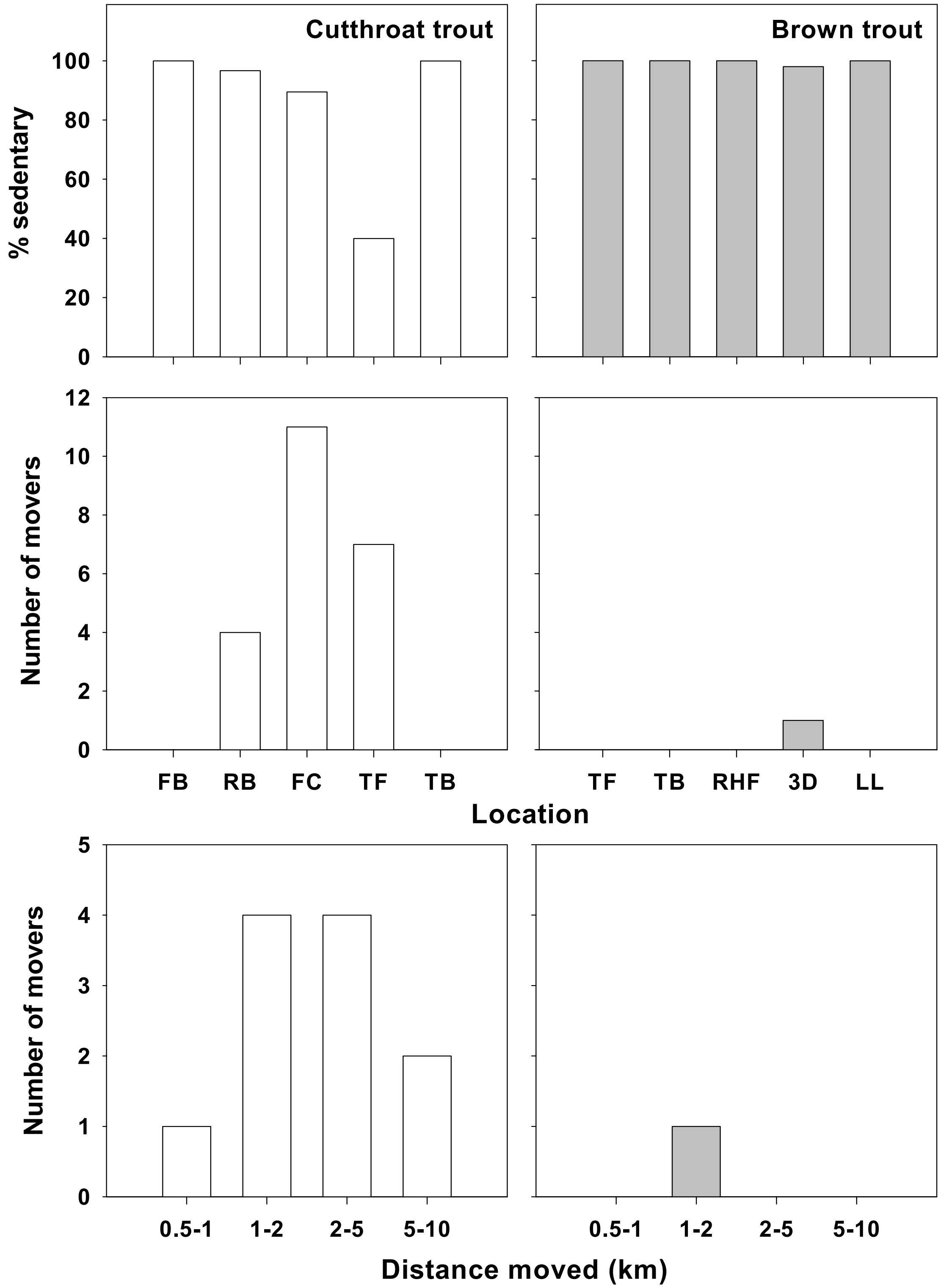


Figure 15. Percentage of cutthroat trout (left panel) and brown trout (right panel) that were recaptured (in 2003) at the location where they were tagged (% sedentary in 2002). FB = Franklin Basin, RB = Red Banks, FC = Forestry Camp, TF = Temple Fork (a tributary), and TB = Twin Bridges. Number of tagged cutthroat trout (left panel) and tagged brown trout (right panel) that moved from the location (x-axis) at which they were tagged in 2002. Distance moved by tagged cutthroat trout (left panel) and brown trout (right panel).

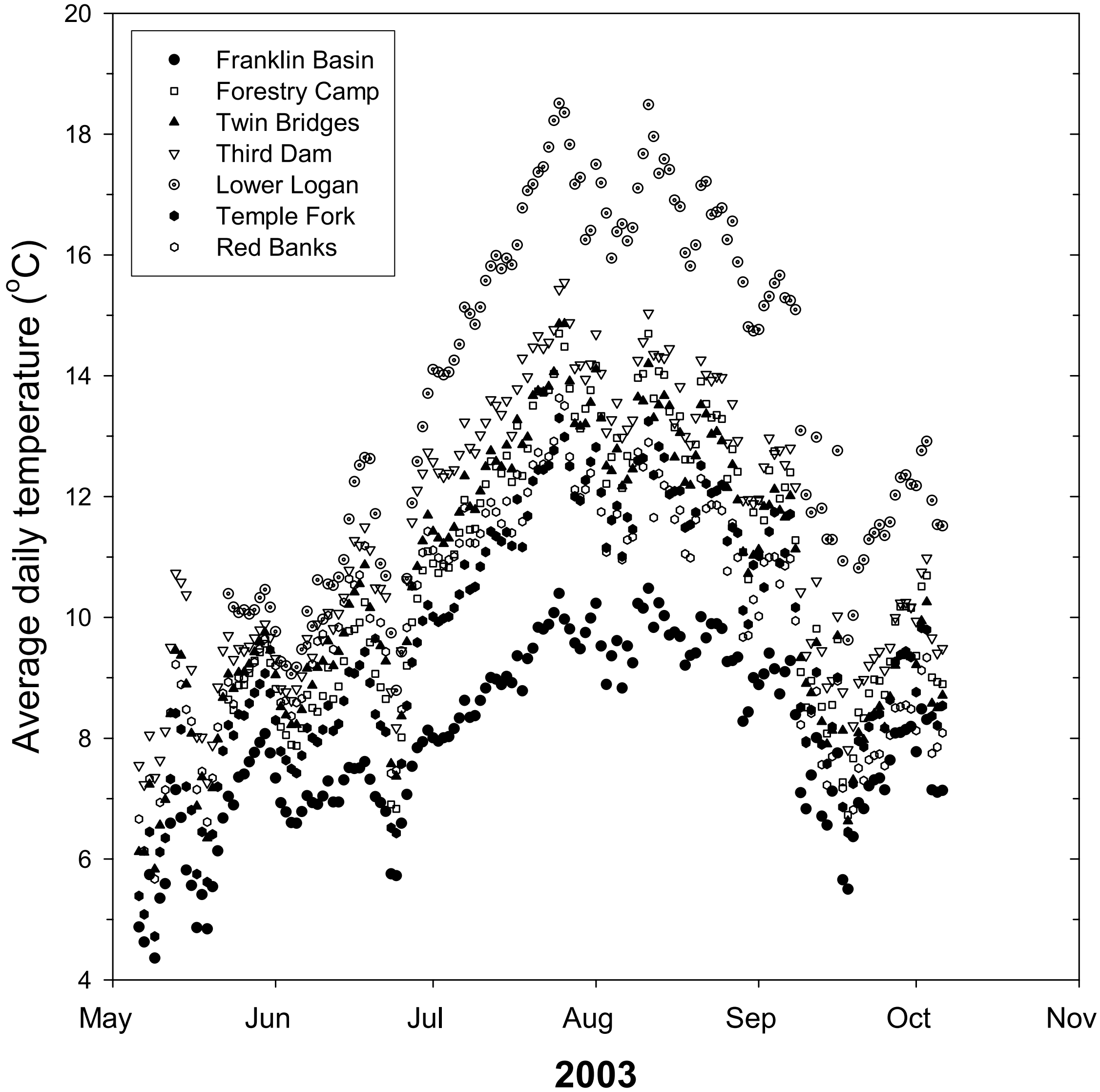


Figure 16. Average daily temperatures at seven sites along the Logan River, May-October 2003. There was no temperature logger placed at Right Hand Fork in 2003.

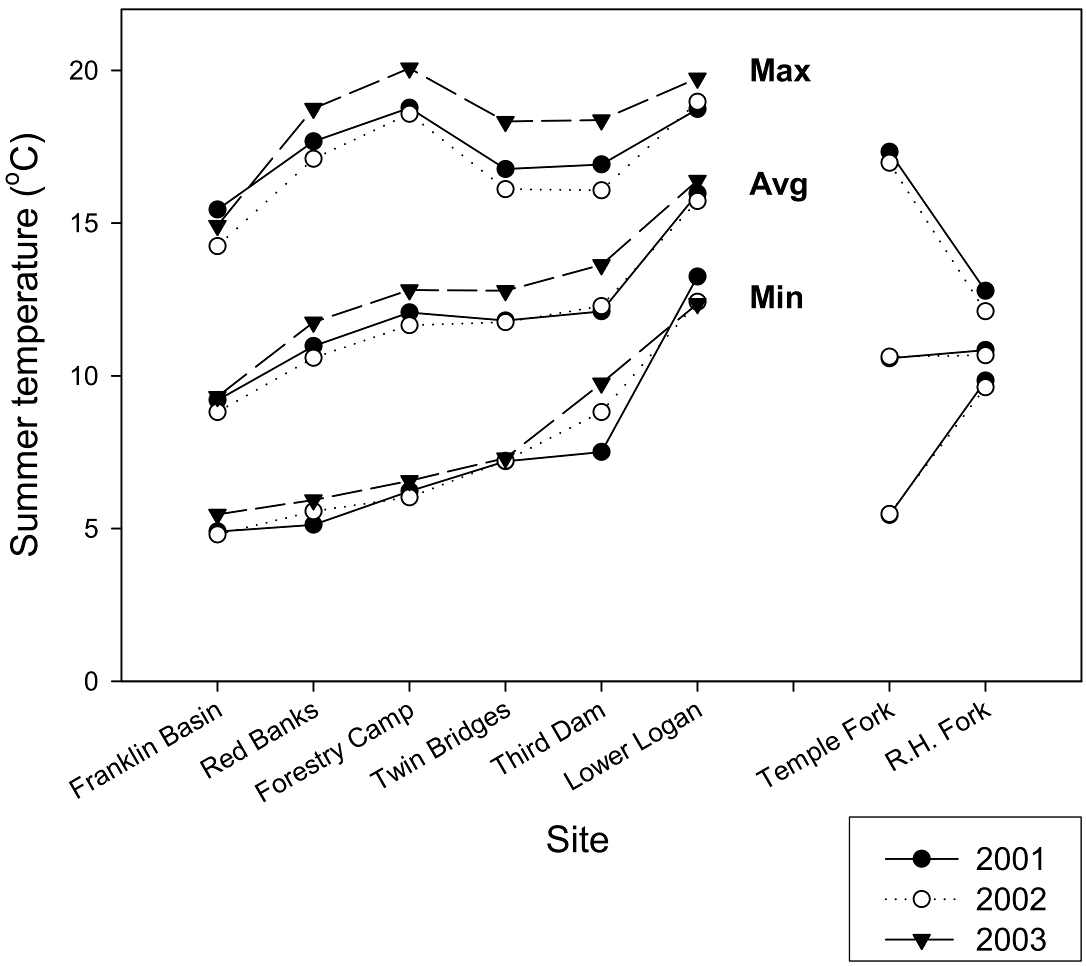


Figure 17. Average summer temperatures at sample sites along the Logan River, 2001-2003. Maximum (Max) and minimum (Min) temperatures are also indicated.

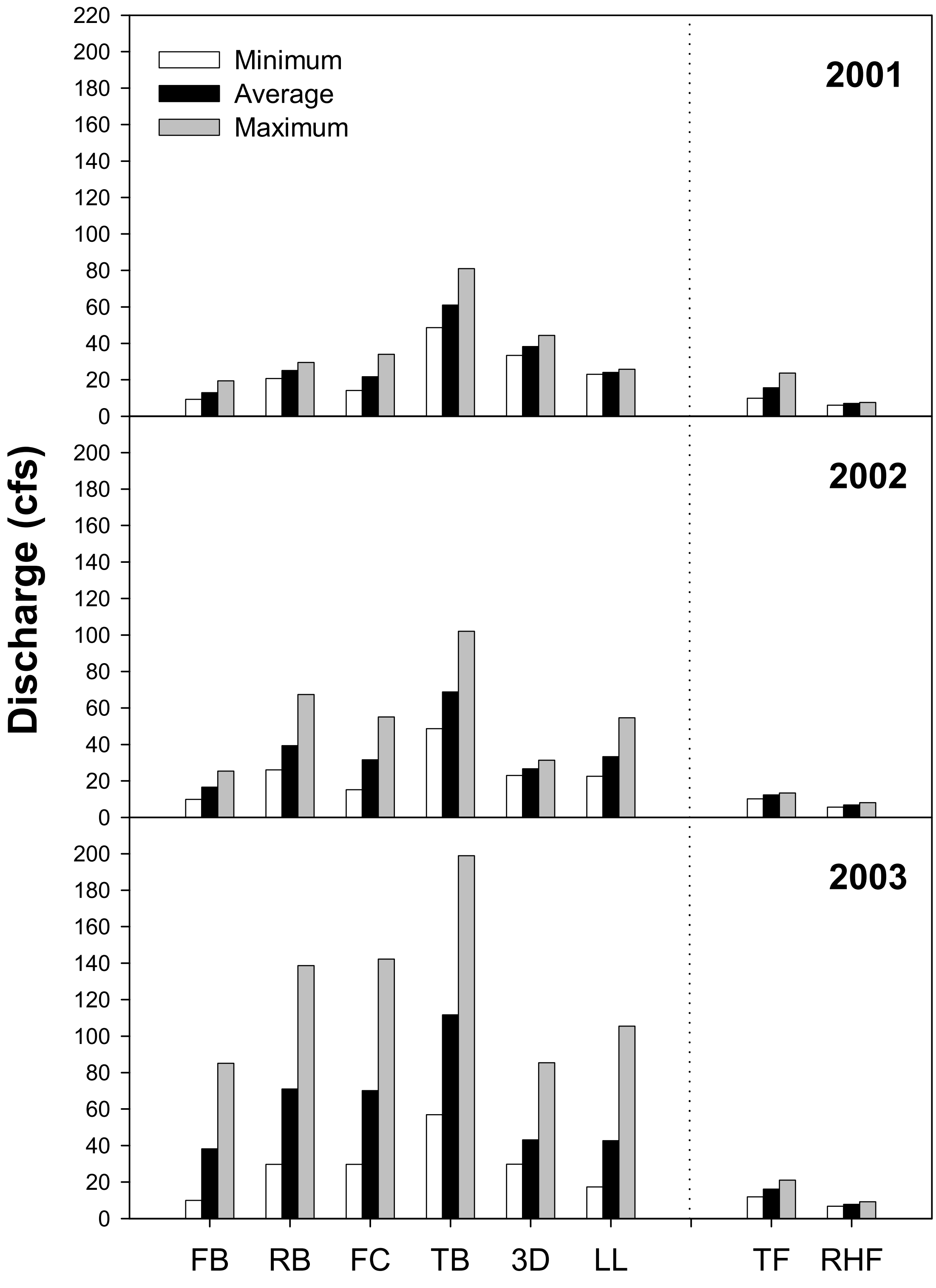


Figure 18. Average summer discharge measurements (cfs) at six sites along the Logan River and two tributaries, 2001- 2003.

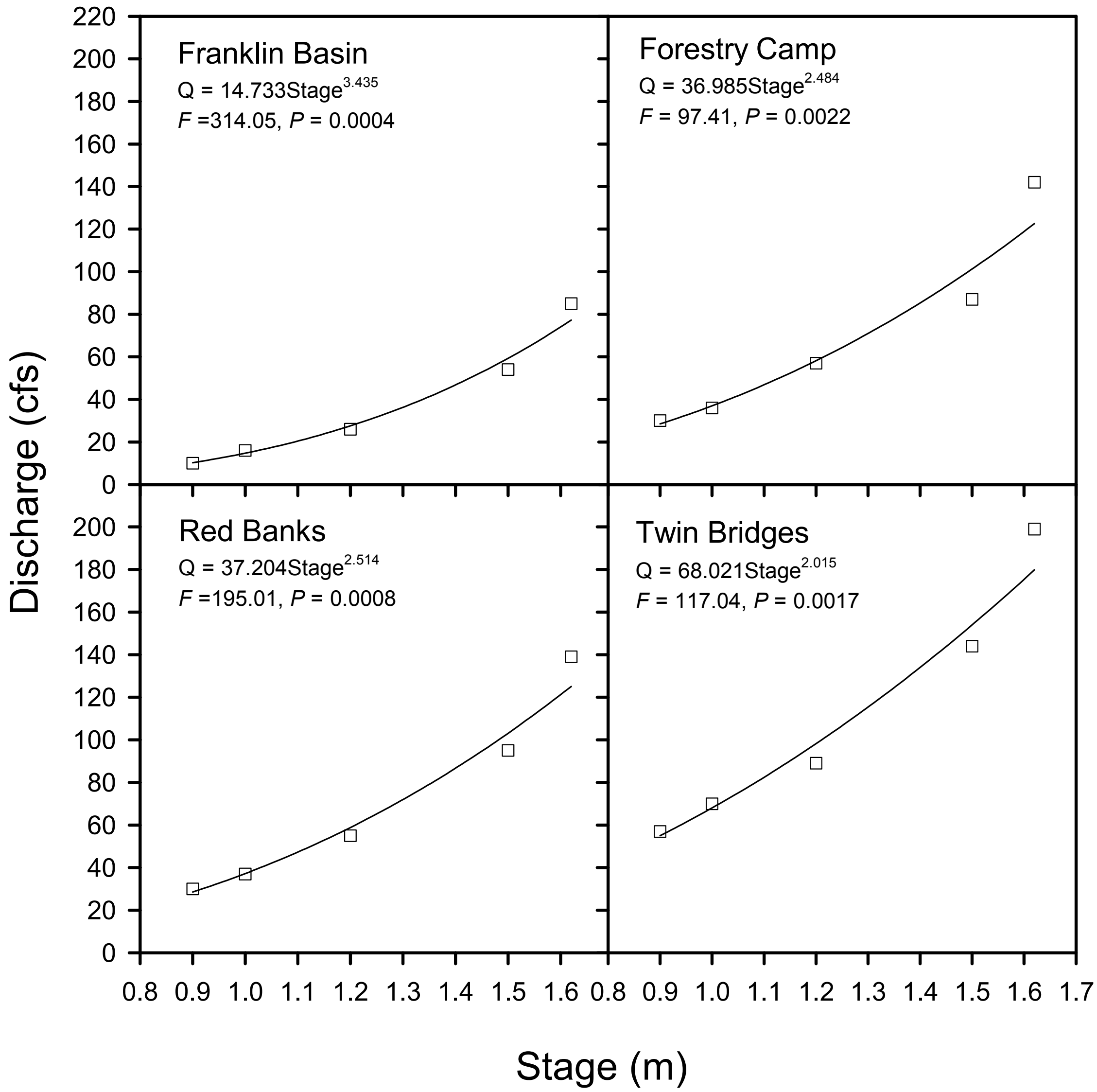


Figure 19. Stage-discharge relationships for the four mainstem sites that are not influenced by irrigation diversions. Regression models explained the variation in flow as a function of water surface elevation at the Franklin Basin bridge well for all sites: Twin Bridges, R^2 = 0.97; Forestry Camp, R^2 = 0.97; Red Banks R^2 = 0.98; Franklin Basin, R^2 = 0.99.

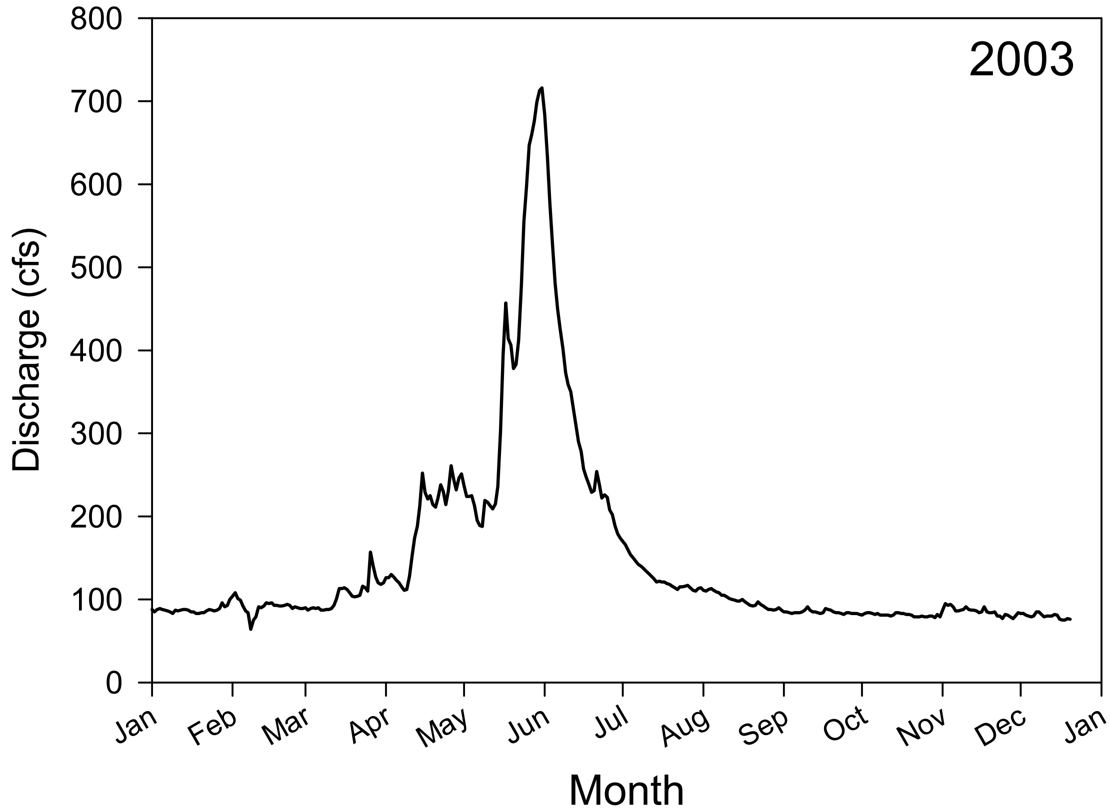


Figure 20. Hydrograph for the Logan River, 2003.

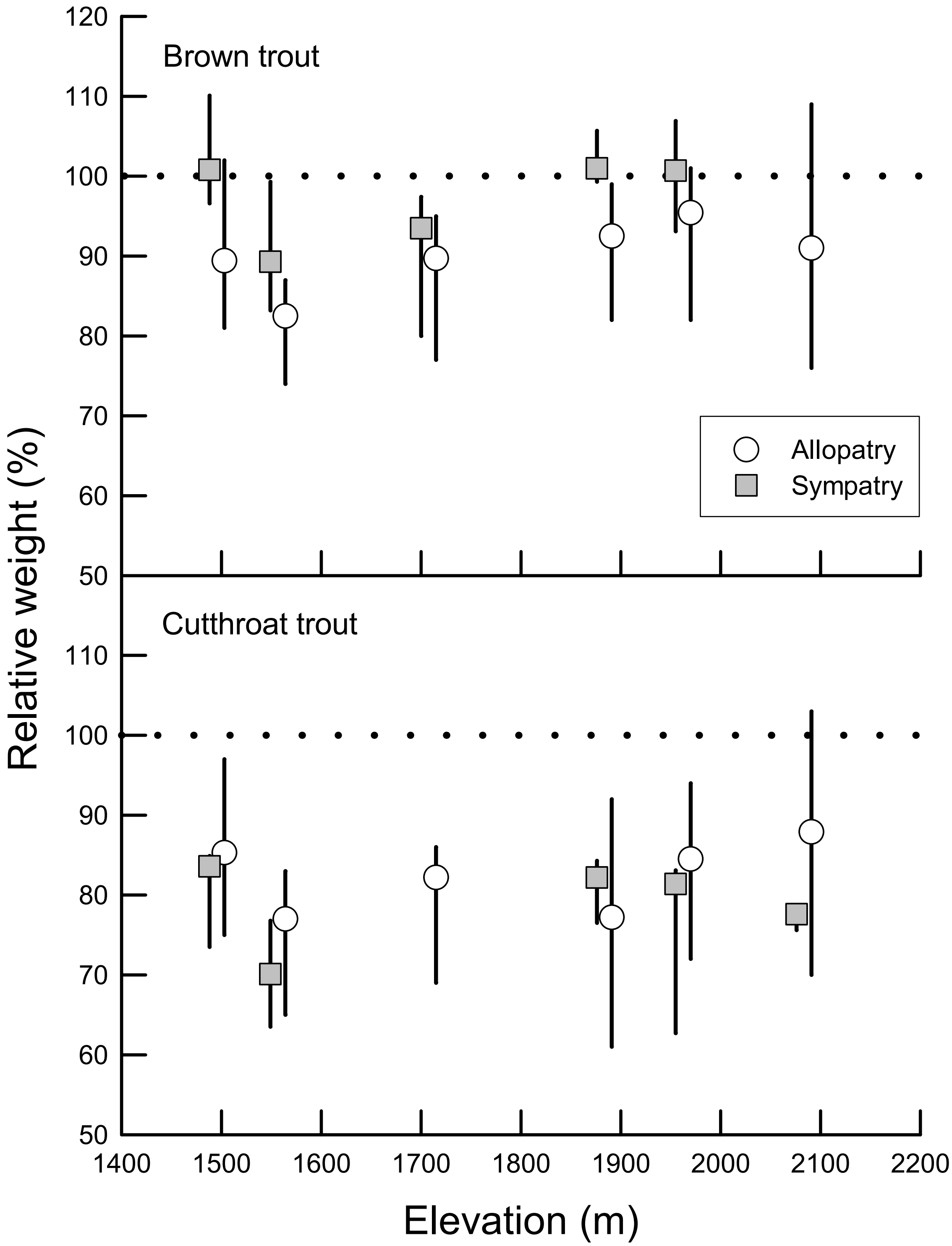


Figure 21. Median (symbols) and range (upper and lower whiskers) of brown trout (top panel) and cutthroat trout (bottom panel) relative weight values plotted as a function of elevation in the Logan River. Circles correspond to enclosures where brown trout were reared in the absence of cutthroat trout (allopatry), while squares represent those where both species were together. For reference, the horizontal line at W_r = 100% indicates that enclosure fish performed as well as wild, river fish. The lowest elevation site corresponds to a site immediately above Second Dam, while the uppermost site is a site ~ 3 km upstream from the US highway 89 crossing near the Logan River – Beaver Creek confluence.

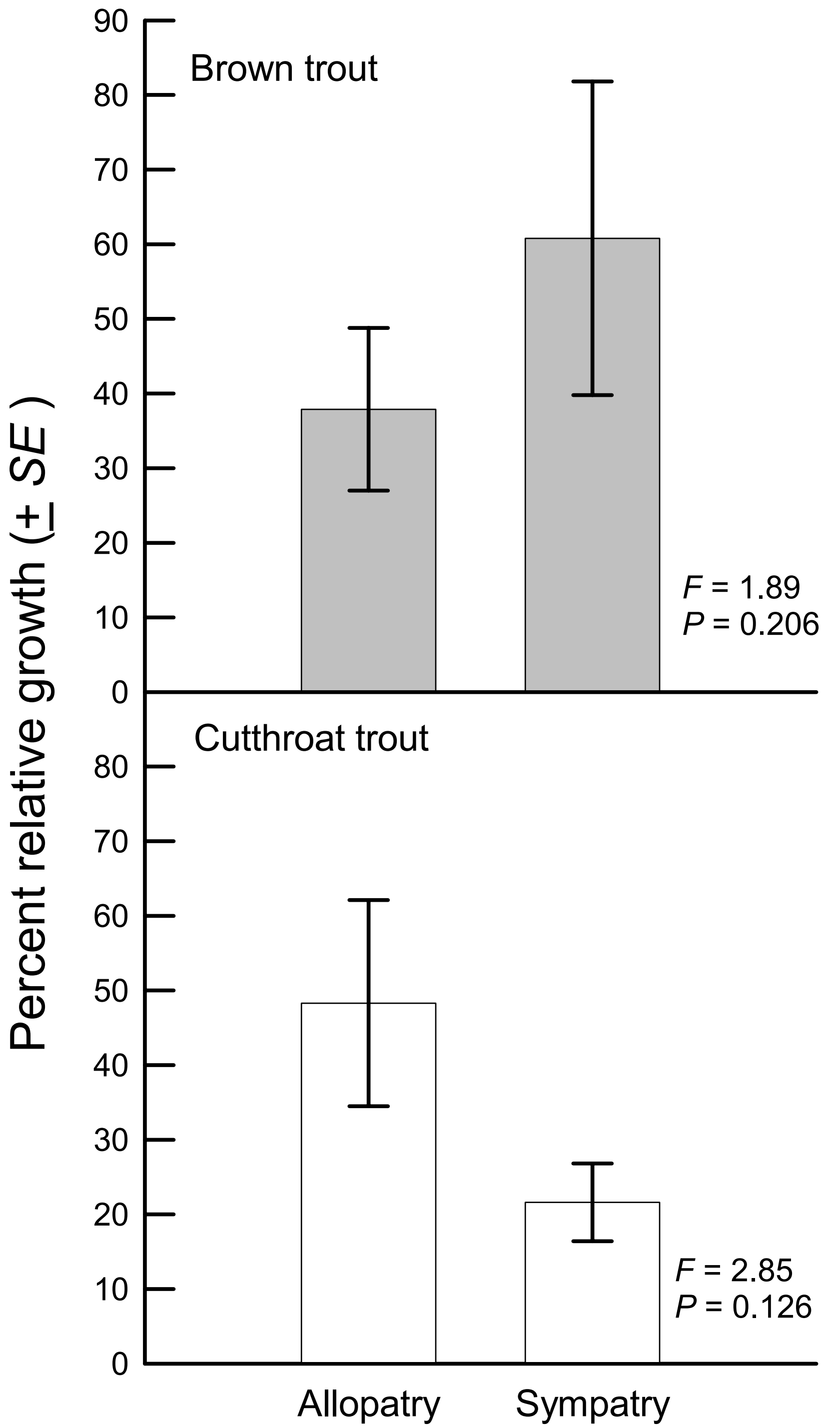


Figure 24. Relative growth (mean ± 1*SE*) for brown trout (upper panel) and cutthroat trout (lower panel) reared in the presence (sympatry) or absence (allopatry) of the other species. *F*-statistics and *P*-values are those from the statistical test (ANOVA or ANCOVA) testing for differences between means. See text for test details.

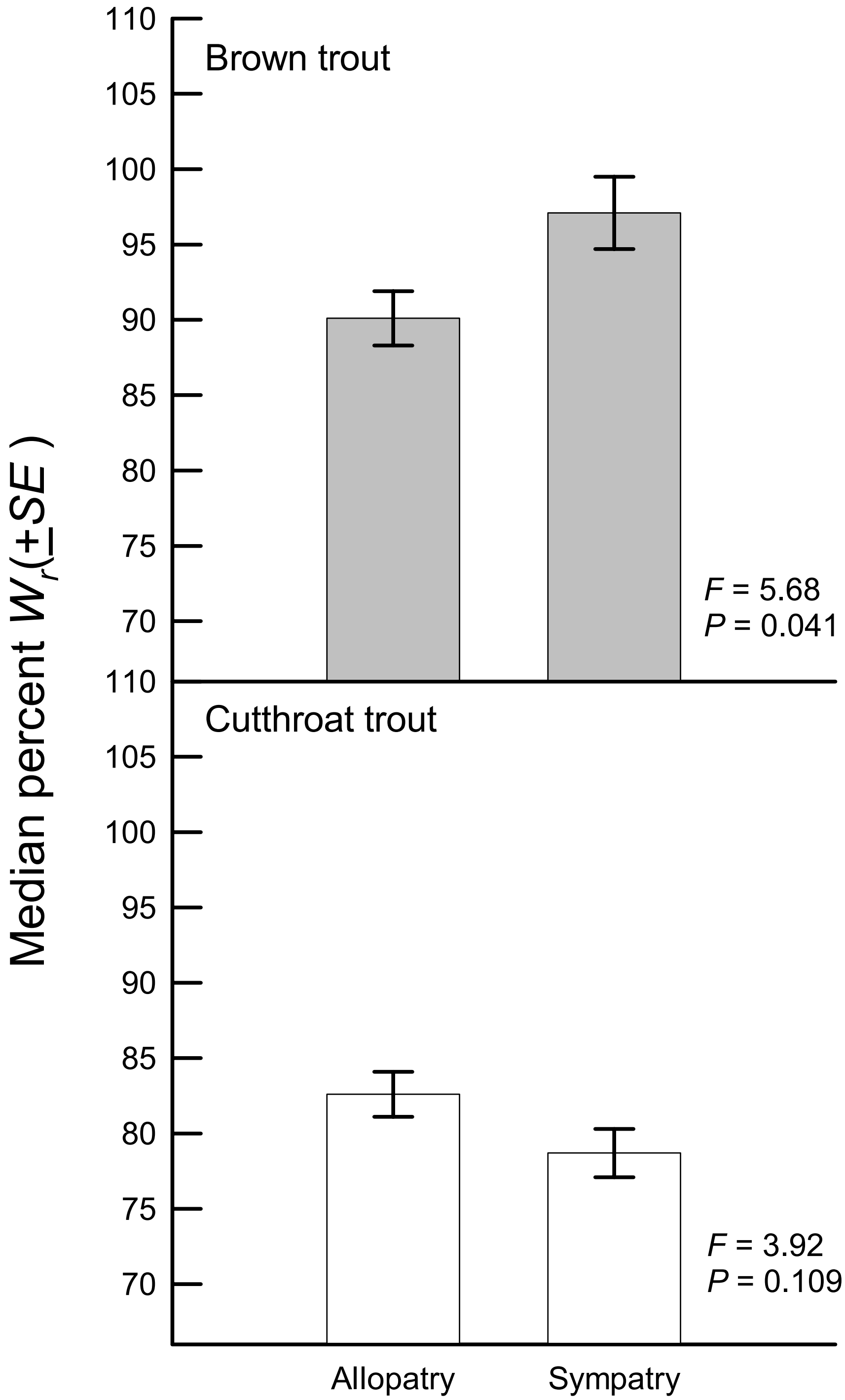


Figure 23. Median relative weight (mean ± 1*SE*) for brown trout (upper panel) and cutthroat trout (lower panel) reared in the presence (sympatry) or absence (allopatry) of the other species. *F*-statistics and *P*-values are those from the statistical test (ANOVA or ANCOVA) testing for differences between means. See text for test details.

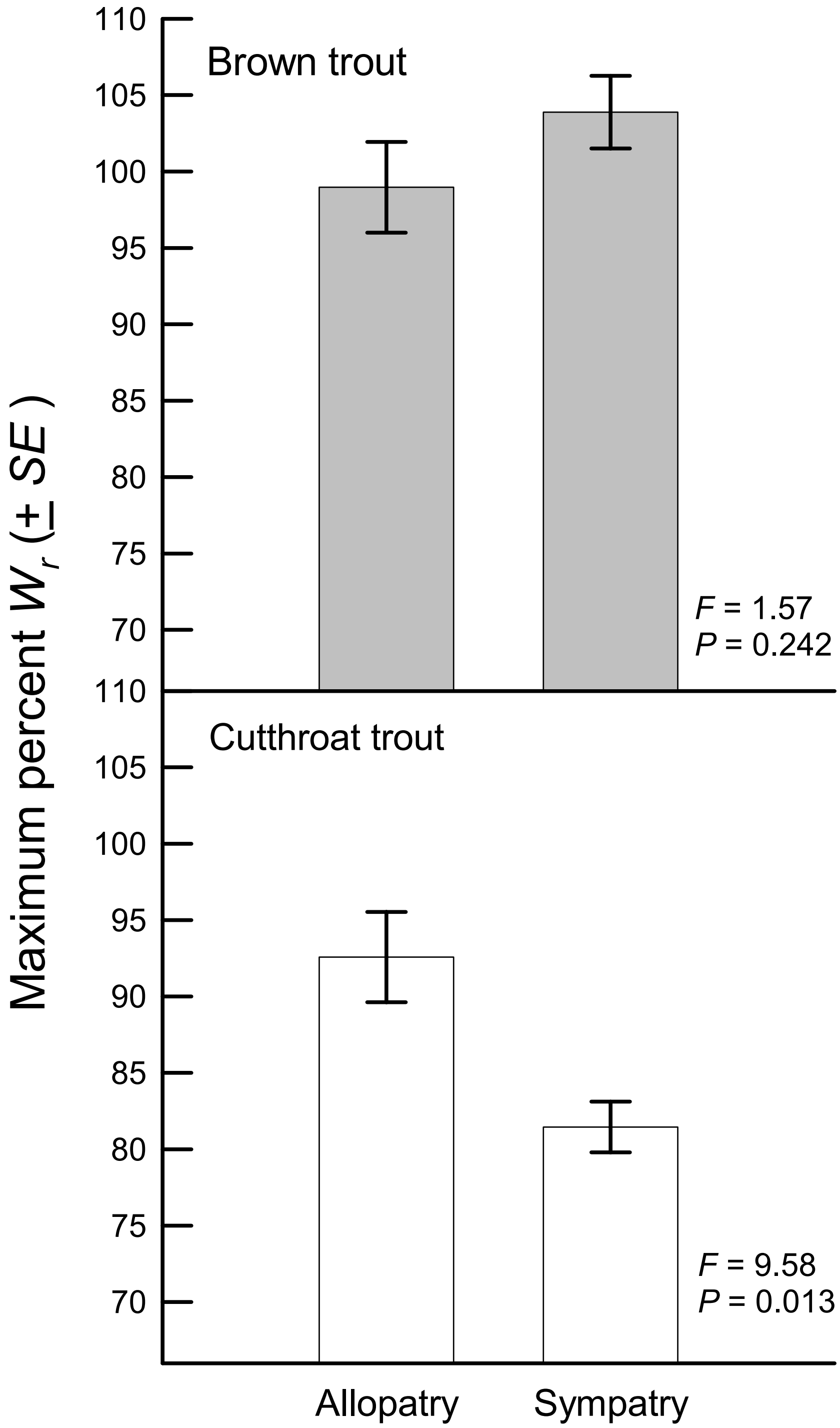
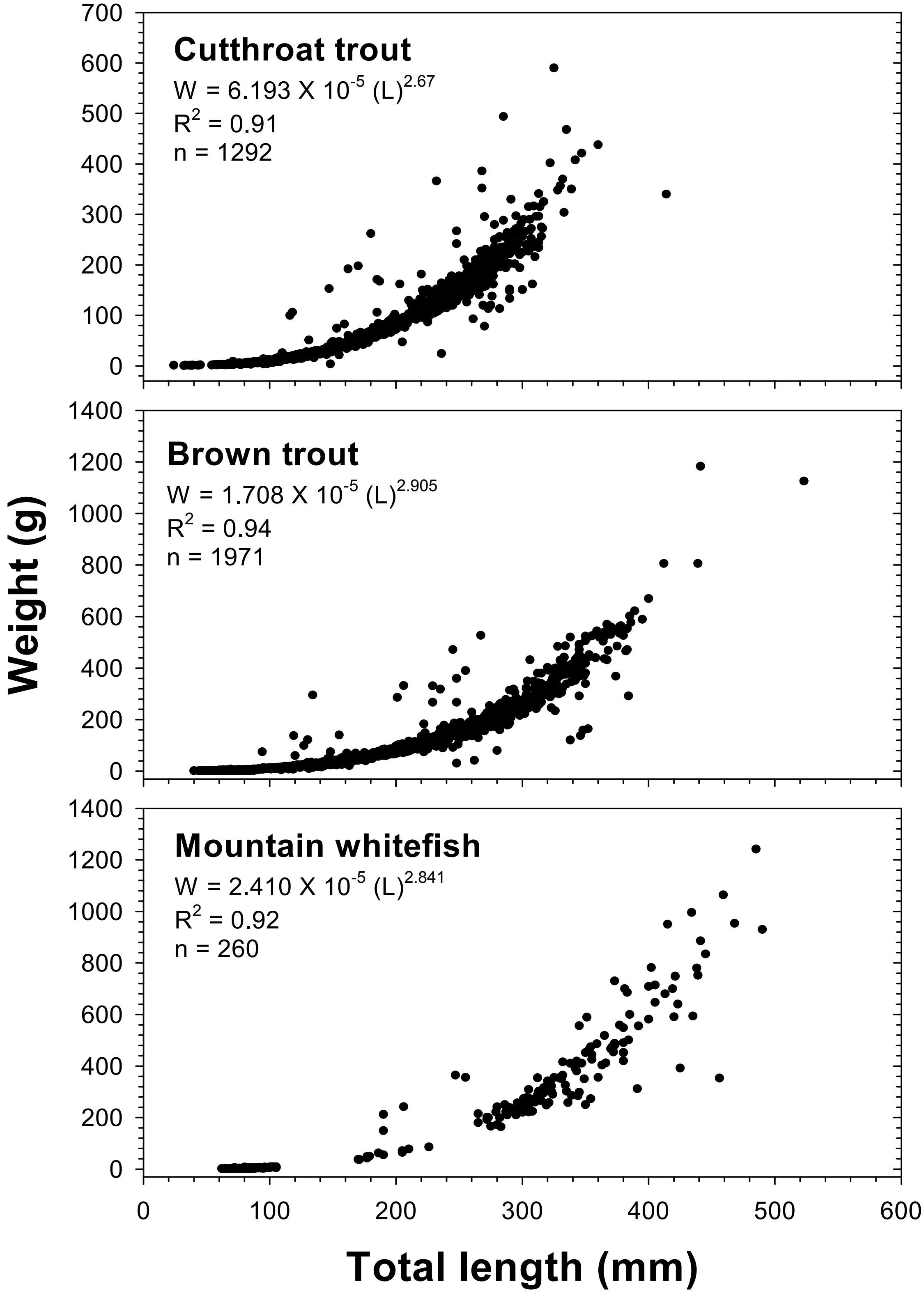
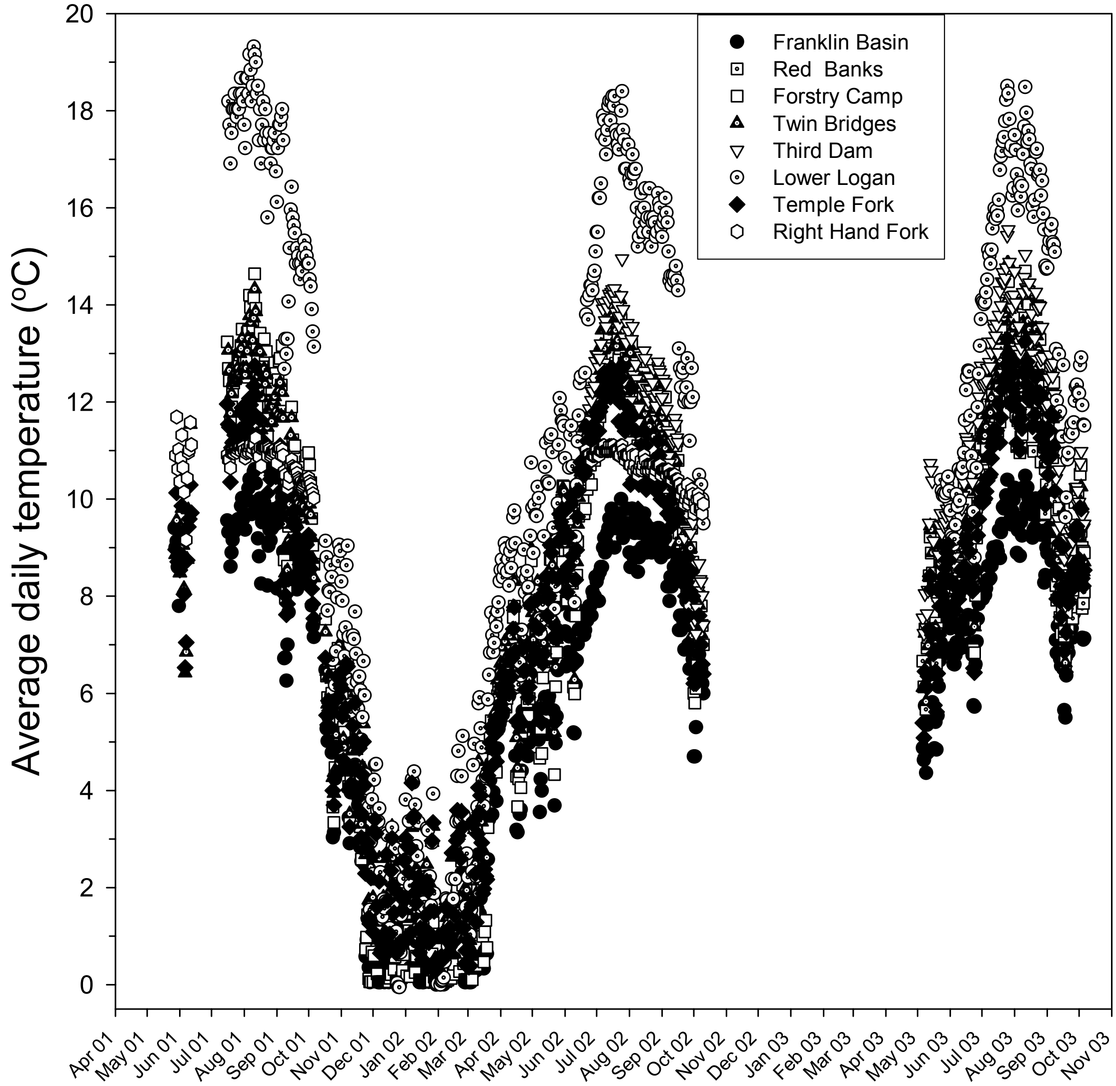


Figure 24. Maximum relative weight (mean ± 1 *SE*) for brown trout (upper panel) and cutthroat trout (lower panel) reared in the presence (sympatry) or absence (allopatry) of the other species. *F*-statistics and *P*-values are those from the statistical test (ANOVA or ANCOVA) testing for differences between means. See text for test details.



Appendix Figure 1. Length-weight regression for cutthroat trout (top panel), brown trout (middle panel), and mountain whitefish (bottom panel) capture in the Logan River, 2001-2003. Regression equations are given along with sample size (n).



Appendix Figure 2. Average daily temperatures at five sites along the Logan River and two tributaries, June 2001 to October 2003.